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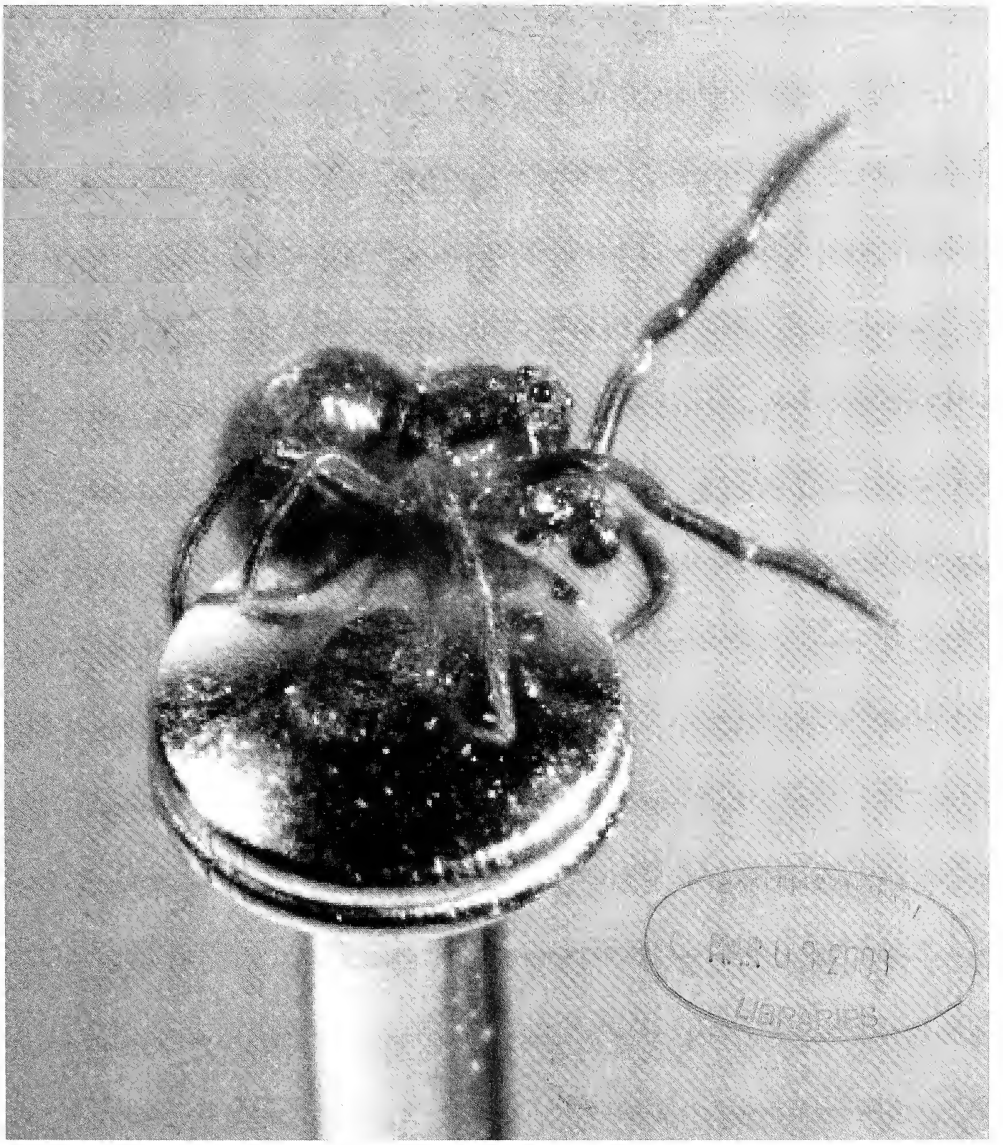

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Cover photo: Male bolas spider *Mastophora cornigera* (Hentz) (Araneae, Araneidae), collected in Riverside County, California, perched on head of a 2-mm diam. pin. Photo by Lenny Vincent.

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ELONGATED PEDICILLATE SETAE: A PUTATIVE SENSORY SYSTEM AND SYNAPOMORPHY OF SPIDERS

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ABSTRACT. We survey spiders from 43 families, 62 genera, and three arachnid outgroups for the presence and diversity of elongated pedicillate setae (EPS)—a complex system of probably sensory setae hitherto undocumented outside Theridiidae. Although not present in all spiders, these setae are sufficiently widespread to suggest they are primitively present in the order. Because they are absent in related arachnids, they appear to be a synapomorphy of spiders. Based on the morphology and orientation of these setae, it has been suggested that they supplement abdominal slit sensilla in proprioception, documenting the position and movement of the abdomen relative to the cephalothorax. Although still poorly known, the presence and distribution of these setae are informative at lower and higher phylogenetic levels.

Keywords: Araneae, phylogeny, proprioreception

Spiders are typically setose and many of the setae, especially on the appendages, are sensory (Seyfarth 1985; Barth 2001). However, the distribution and function of the many different kinds of setae on spider bodies are poorly known. Morphological, behavioral, histological, and neurobiological research are all necessary to understand setal distribution, function, and to establish interspecific homologies. Morphology can document apparently different types of setae and their distribution on individuals as well as across species. It can also infer function from their detailed structure, distribution, and orientation. Agnarsson (2004) documented the distribution of distinct elongated setae around the pedicel on abdomens of theridiid spiders. The distribution of these setae was phylogenetically informative. They surround the pedicel and are juxtaposed to the cephalothorax so that abdominal movement is likely to cause flexion, which may, in turn, signal the relative positions of the abdomen and cephalothorax. He proposed the name "suprapedicillate proprioceptive setae:" proprioception (or proprioreception) is the perception of the body's position and movement including physical displacement and any changes in tension, or force within the body (e.g., Seyfarth & Pflügler 1984; Seyfarth 1985; Seyfarth et al. 1985).

The proprioceptive hypothesis was based on the morphological, not behavioral, histological, and neurobiological evidence. Here we use a more neutral term, elongated pedicillate setae (EPS) although we hope that the hypothesis of proprioceptive function will be tested in future studies.

Agnarsson's (2004) survey was limited to theridiids and a few outgroups and his discussion focused mainly on their phylogenetic utility within theridiids. Here we document the distribution of EPS and their potential as characters for higher level phylogenetic studies from a broader survey of spider families.

METHODS

Sixty-nine taxa were selected to span the order Araneae and closely related outgroups (many additional species, especially theridiids, were surveyed by Agnarsson 2004). Taxon representation was biased, however, towards Orbiculariae, and Theridiidae by the authors' specialties. Given sufficient specimens, the abdomens were critical point dried, glued to a rivet, and sputter coated with Au/Pd.

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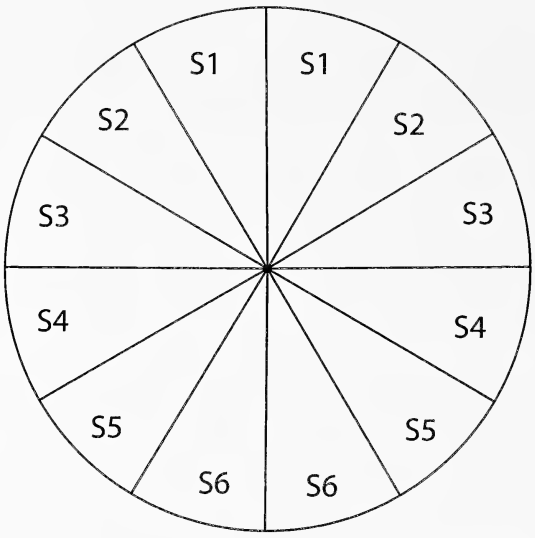


Figure 1.—The six symmetric sectors around the pedicel in which the distribution of EPS were scored.

Scanning electron micrographs were taken of the area around the pedicel from a standard view (normal to the pedicel axis) and other angles when deemed useful. At this rudimentary stage of knowledge, homology of individual setae or setal groups remains ambiguous, so we simply divided the pedicel area into six (paired) sectors, and tabulated the presence and number of EPS in each (Fig. 1). Two people independently scored presence/absence of EPS in each SEM photograph; if any disagreement occurred between the two the taxon in question was scored as "uncertain."

Among Araneae outgroups where EPS seem to be completely absent, presence or absence was verified under a dissecting microscope. For rare taxa (e.g., *Liphistius*) we did not score their distribution because standard view photographs were not available.

RESULTS

The phylogenetic distribution of EPS is given in Table 1 and Figure 2. Three arachnid orders, Amblypygi, Uropygi, and Palpigradi share a narrow pedicel with Araneae, but the pro/opisthosoma connection in spiders is especially flexible, probably to promote mobility of the spinnerets. Amblypygids, uropygids, and schizomids apparently lack EPS. EPS appear to be present in all major spider lineages (Mesothelae, Mygalomorphae, and Araneomorphae). Many of the examined taxa had at least one pair of proprioceptive setae (Figs. 2–36, Table 1).

The distinctiveness of EPS varies widely across spiders. In some taxa, including nearly all examined orbicularians, EPS are easily distinguished from other abdominal setae by the morphology of the robust socket (Fig. 8) and shaft, which is unusually long, slender, and smooth (Figs. 3–36). Their number and position are therefore fairly easy to score (Figs. 3–5). In *Deinopis* and some non-orbicularians the EPS can be distinguished because they are mostly smooth, in contrast to the otherwise serrate or plumose (feathery) abdominal setae (Fig. 30–36). In many other cases, however, the distinction between proprioceptive and other abdominal setae was not clear, and the two scorers often disagreed, usually on their position or number rather than presence or absence. Taxa in which even the existence of EPS was unclear are labeled with parentheses as "uncertain" in Table 1. Given these doubts, for consistency Table 1 indicates only the presence and relative abundance, rather than counts, of EPS in each sector.

Dividing the pedicel region into six radial sectors is purely heuristic. To reify these "sectors" by treating them as biologically meaningful would be a mistake. With that in mind, one can nevertheless use the sector notation simply as a vocabulary to speculate about patterns. Whether uncertainties are counted as presences or absences, the same ten patterns occur: 1-2, 1-2-3, 1-3, 2-3, 2, 3, 3-4, 2-3-4, 1-2-3-4, and 1-2-3-4-5. This is nearly half of the 26 ways 5 digits may be combined. More fundamentally, the two evident axes of variation are extension (some taxa have a more extensive ring of EPS than others), and position (relatively dorsal or ventral). No strongly disjunct groups of setae were observed, e.g. 1-4, 1-5, 2-6, etc. Given the sparse sample, such diversity is not encouraging, but within families the variation may be more regular and informative, as was the case with Theridiidae (Agnarsson 2004, 2006).

DISCUSSION

At this point it seems that EPS is a synapomorphy of spiders and evolved in their common ancestor co-extensively with the increased flexibility of the prosoma-opisthosomal articulation. This supports Agnarsson's (2004) hy-

Table 1.—The distribution of EPS in various arachnid taxa by abdominal "sector" (see Fig. 1). "x" indicates one to few setae, "xx" indicates few to many setae, and parentheses indicate uncertainty. Detail of locality information represents information on collection label. All specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC. *In *Pardosa* sp. and *Gnaphosa parvula* proprioceptive setae were scored absent by both examiners, however, as discussed in text it is difficult to rule out EPS in these species as they may be hidden by a brush of other seta (see Figs. 41–44).

Family (ORDER)	Major clade	Species	EPS	Sector					Locality
				1	2	3	4	5	
AMBLYPYGI	AMBLYPYGI	*Phrynus longipes* (Pocock, 1894)	Absent	n/a					Puerto Rico, 22.xii.1989
SCHIZOMIDA	SCHIZOMIDA	indet.	Absent	n/a					Marshall Island, 1.i.1977, D.A. Anderson
UROPYGI	UROPYGI	Thelyphonidae indet.	Absent	n/a					USA, Florida, 14.ii.1997.
Liphistiidae	Mesothelae	*Liphistius malayanus* Abraham, 1923	Present	n/a					Malaysia, Pahang, Cameron Highlands, 3–4.vi.1981, W. Sedgwick.
Antrodiaetidae	Mygalomorphae	*Antrodiaetus robustus* (Simon, 1891)	Present	n/a					USA, Preston Co., WV, 26.vi-3.vii.1989, D.T. Jennings
Atypidae	Mygalomorphae	*Atypus muralis* Bertkau, 1890	Uncertain	n/a					Russia, Samara Area Zhiguli Reservation, viii.1981, V.I. Ovtsharenko
Dipluridae	Mygalomorphae	*Ischnothele digitata* (O. P.-Cambridge, 1892)	Present	n/a					Mexico, Los Cocos, Vera Cruz, viii.1908, A. petrunkevitch
Hypochilidae	Hypochilidae	*Hypochilus pococki* Platnick, 1987	Present	(x)	x	-	-	-	USA, Macon Co., NC, 5.ix.1990, J. Coddington
Austrochilidae	Austrochilidae	*Thaida peculiaris* Karsch, 1880	Present	x	x	-	-	-	Chile, Llanquihue Prov., P.N. Vincent P. Rosales, 24–26.xii.2000, J. Miller et al.
Filistatidae	Haplogynae	*Kukulcania hibernalis* (Hentz, 1842)	Present	(x)	x	x	x	-	USA, St. Lucie Co., Florida, 25.ii.1986, P.M. Mikkelsen.
Dysderidae	Haplogynae	*Dysdera crocata* C.L. Koch, 1838	Uncertain	(x)	-	-	-	-	USA, Maryland, Baltimore Co., 17.i.1987, W.E. Steiner et al.
Oonopidae	Haplogynae	sp. "ONO01"	Uncertain	(x)	-	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Scytodidae	Haplogynae	*Scytodes thoracica* (Latreille, 1802)	Present	x	xx	x	-	-	USA, New Britain, 13.vi.1961, B.J. Kaston.
Pholcidae	Haplogynae	*Mesabolivar aurantiacus* (Mello-Leitão, 1930)	Absent	-	-	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Sicaridae	Haplogynae	*Loxosceles deserta* Gertsch, 1973	Present	xx	xx	-	-	-	USA, Utah, Washington Co., 25.viii–9.ix.1991, W.E. Steiner
Eresidae	Eresoidea	*Stegodyphus* sp.	Absent	-	-	-	-	-	Myanmar, Chattin Wildlife Sanctuary, Sagaing Div., 7–12.x.1998, Coddington & Babtista.
Oecobidae	Eresoidea	*Oecobius navus Blackwall, 1859*	Uncertain	-	(x)	-	-	-	no data
Palpimanidae	Palpimanoidea	*sp.* (palpinanid sp 1)	Absent	-	-	-	-	-	Tanzania, Iringa Distr., Uzungwa Scarp Forest, 17–27.v.1997
Malkaridae	Palpimanoidea	*Chilenodes australis* Platnick and Forster, 1987	Absent	-	-	-	-	-	Chile, Puyhue National Park, vii. 2000, I. Agnarsson and J. Miller
Archaeidae	Palpimanoidea	*Eriauchenius vadoni* (Millot, 1948)	Absent	-	-	-	-	-	Madagascar, Steiner
Titanoecidae	Entelegynae	*Titanoeca brunnea* Emerton, 1888	Present	-	-	x	-	-	USA, Sleepy Creek Hunt & Fish Area, Berkeley Co., 16–23.v.1986, P.J. Martinat.
Agelenidae	Entelegynae	*Agelenopsis pennsylvanica* (C.L. Koch, 1843)	Present	xx	xx	xx	-	-	USA, Washington DC, 1.x.1985, K. Smith.
Amaurobidae	Entelegynae	*Amaurobius sp.*	Uncertain	-	-	(x)	-	-	USA, Piscataquie County, Maine, 1.vi.1978. D.T. Jennings & M.WL Houseweart.
Dictynidae	Entelegynae	*Dictyna major* Menge, 1869	Absent	-	-	-	-	-	Russia, Siberia
Oxyopidae	Entelegynae	*Oxyopes salticus* Hentz, 1845	Present	x	x	x	-	-	USA, Massachusetts, Barnstable Co., 2.vi.1989. R.L. Edwards

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Lycosidae	Entelegynae	*Pardosa* sp.	Absent*	-	-	-	-	-	USA, Louisiana
Anyphaenidae	Entelegynae	*Anyphaena* sp.	Present	(x)	-	(x)	-	-	USA, Rock Creek Park, Washington DC, 3.vii.1985, J. Coddington.
Thomisidae	Entelegynae	*Tmarus* sp.	Present	x	x	x	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Clubionidae	Entelegynae	*Clubiona obesa* Hentz, 1847	Uncertain	(x)	(x)	-	-	-	USA, Ellicott Rock Wilderness Area, Rabun Co., Georgia, 20.v.1993, Bond et al.
Gnaphosidae	Entelegynae	*Gnaphosa parvula* Banks, 1896	Absent*	-	-	-	-	-	USA, Maine
Salticidae	Entelegynae	*Lyssomanes taczanowski* Galiano, 1980	Present	x	x	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Deinopidae	Orbiculariae	*Deinopsis* sp.	Present	-	xx	xx	-	-	Guyana, Bartika, 20.vii.1999, I. Agnarsson and M. Kunter
Uloboridae	Orbiculariae	*Uloborus trilineatus* Keyserling, 1883	Uncertain	-	(x)	-	-	-	Peru, Madre de Dios, Tambopata. 9.vi.1988. J. Coddington (NMNH)
Uloboridae	Orbiculariae	*Philioponella* sp. ("sp. 6")	Present	-	x	x	-	-	Costa Rica, Heredia Prov., Puerto Viejo, La Selva Biological station, 3–5.iv.1989, J. Coddington.
Araneidae	Orbiculariae	*Araneus alboventris* (Emerton, 1884)	Present	-	x	x	-	-	USA, Rock Creek Park, Washington DC, 7.vii.1985, J Coddington
Araneidae	Orbiculariae	*Argiope argentata* (Fabricius, 1775)	Present	-	x	x	-	-	Peru, Madre de Dios, Silva and Coddington
Araneidae	Orbiculariae	*Eustala* sp.	Present	-	x	x	-	-	Guyana, Bartika, 20.vii.1999, I. Agnarsson
Araneidae	Orbiculariae	*Pronous tuberculifer* (Keyserling, 1881)	Present	-	x	x	-	-	Guyana, Bartika, 20.vii.1999, I. Agnarsson and M. Kunter

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Nephilidae	Orbiculariae	*Nephila* inaurata (Walckenaer, 1842)	Present	-	x	xx	-	-	Madagascar, Ranamofana National Park, iv. 2001, I. Agnarsson and M. Kunter
Tetragnathidae	Orbiculariae	*Leucauge venusta* (Walckenaer, 1842)	Present	(x)	x	x	-	-	USA, Rock Creek Park, Washington DC, 16.vii.1985, J. Coddington
Tetragnathidae	Orbiculariae	*Meta segmentata* (Clerck, 1757)	Present	-	-	xx	-	-	Denmark, Hestehaven, 30.viii.1994, Coddington et al.
Cyatholypidae	Orbiculariae	*Isicabu henriki* Griswold, 2001	Present	-	-	x	x	-	Tanzania, Iringa Distr. Uzungwa Scarp Forest Reserve, 17–27.v.1997. Coddington et al.
Synotaxidae	Orbiculariae	*Synotaxus waiwai* Agnarsson, 2003	Present	x	x	x	x	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Synotaxidae	Orbiculariae	*Physoglenes puyehue* Platnick, 1990	Absent	-	-	-	-	-	Chile, Puyhue National Park, vii. 2000, I. Agnarsson and J. Miller
Synotaxidae	Orbiculariae	*Chileotaxus sans* Platnick, 1990	Present	x	x	x	x	-	Chile, Puyhue National Park, vii. 2000, I. Agnarsson and J. Miller
Mimetidae	Orbiculariae	*Mimetus interfector* Hentz, 1850	Present	-	x	x	-	-	USA, Florida, J. Coddington
Nesticidae	Orbiculariae	*Eidmanella pallida* (Emerton, 1875)	Present	-	x	x	x	-	Trinidad, 1988, Coddington
Theridiidae	Orbiculariae	*Latrodectus geometricus* C.L. Koch, 1841	Present	x	x	x	x	x	Madagascar: Berenty reserve, 2.v.2001, Agnarsson & Kuntner
Theridiidae	Orbiculariae	*Anelosimus vittatus* (C.L. Koch, 1836)	Present	x	x	x	xx	-	Slovenia, Sembpas, 1998, Kuntner et al.
Theridiidae	Orbiculariae	*Anelosimus biglebowski* Agnarsson, 2006	Present	x	x	x	x	-	Tanzania, Iringa District, Uzungwa Scarp forest, 17–27.v.1997, Scharff et al.
Theridiidae	Orbiculariae	*Ariamnes attenuatus* O. P.-Cambridge, 1881	Present	x	xx	x	-	-	Peru, Madre de Dios, Pakitza, 2.x.1987, Silva & Coddington

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Theridiidae	Orbiculariae	*Dipoena nr. hortoni*	Present	-	x	x	x	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Theridiidae	Orbiculariae	*Episinus maculipes* Cavanna, 1876	Present	(x)	x	x	x	-	Slovenia, Sembpas, 1998, Kuntner et al.
Theridiidae	Orbiculariae	*Faiditus cf. caudatus*	Present	x	-	x	-	-	Colombia, Iguaque, 2850–3000 m, 5.ii.1998, Hormiga et al.
Theridiidae	Orbiculariae	*Kochiura rosea* (Nicolet, 1849)	Present	x	x	x	x	-	Chile, Juan Fernandez Islands, Mas Afuera, Quebrada Vaca, 22.iii.1962, Malkin
Theridiidae	Orbiculariae	*Rhomphaea metaltissima* Soares & Camargo, 1948	Present	x	x	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Theridiidae	Orbiculariae	*Spintharus flavidus* Hentz, 1850	Present	x	x	x	x	-	Costa Rica, Cartago, RF de Rio Macho, 22–26.iii.1999, Miller.
Theridiidae	Orbiculariae	*Ameridion nr. petrum*	Present	x	x	x	x	-	Costa Rica, Cartago, Reserva forestal de Rio Macho, 2850 m. 22–26.iii.1999, Zujko-Miller
Theridiidae	Orbiculariae	*Theridion varians* Hahn, 1833	Present	x	x	x	x	-	Slovenia, 23.vii.1999,
Theridiidae	Orbiculariae	*Theridion frondeum* Hentz, 1850	Present	x	x	x	x	-	USA, Montgomery Co., MD, 30.v.1985, Smith.
Pimoidae	Orbiculariae	*Pimoa breviata* Chamberlin and Ivie, 1943	Present	-	x	x	xx	-	USA, California
Linyphiidae	Orbiculariae	*Linyphia triangularis* (Clerck, 1757)	Present	-	x	xx	x	-	Denmark, Hestehaven, 30. viii. 1994, Coddington et al.
Linyphiidae	Orbiculariae	*Frontinella communis* (Hentz, 1850)	Present	x	x	x	x	-	USA, Rock Creek Park, Washington DC, J. Coddington

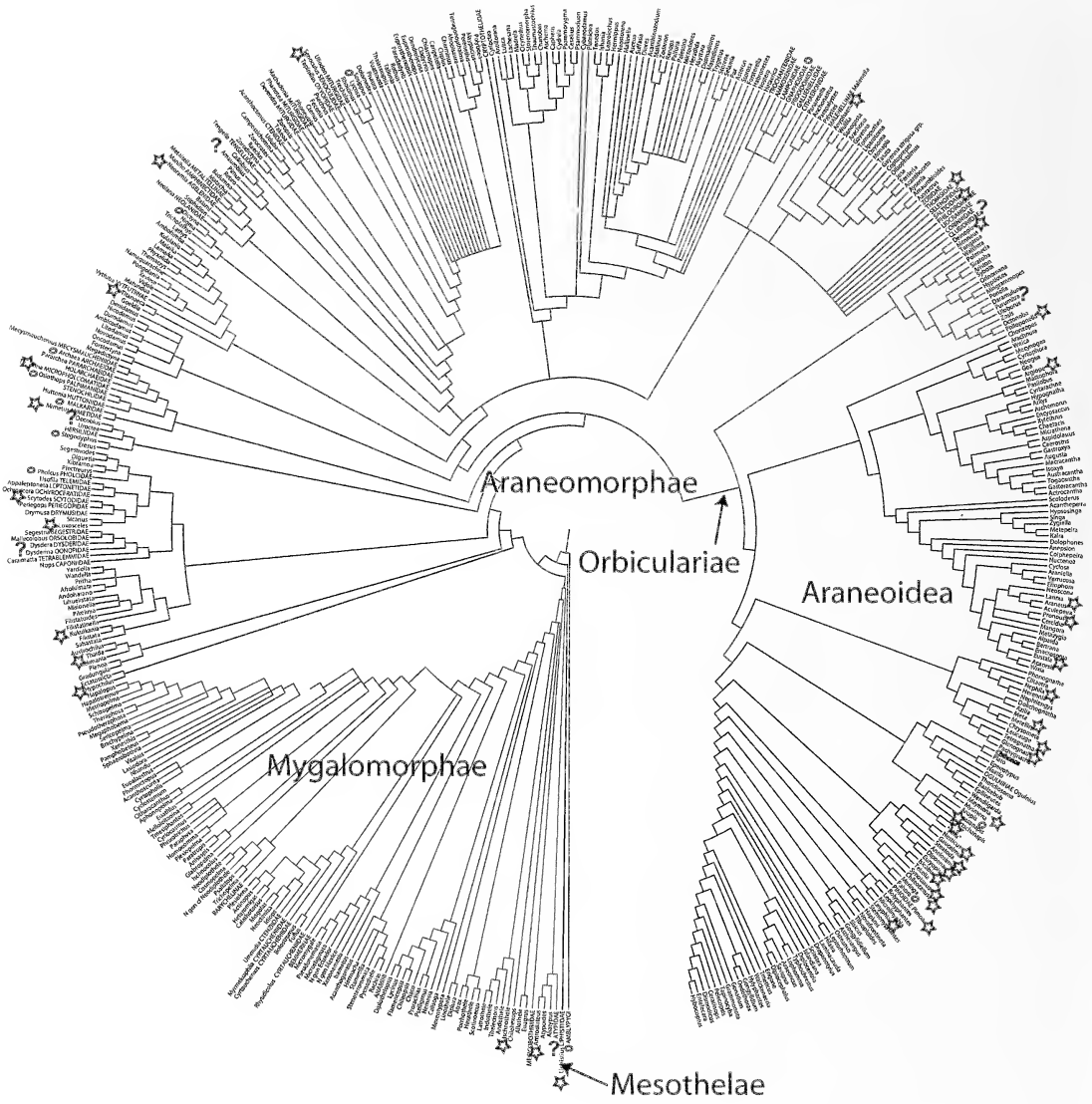
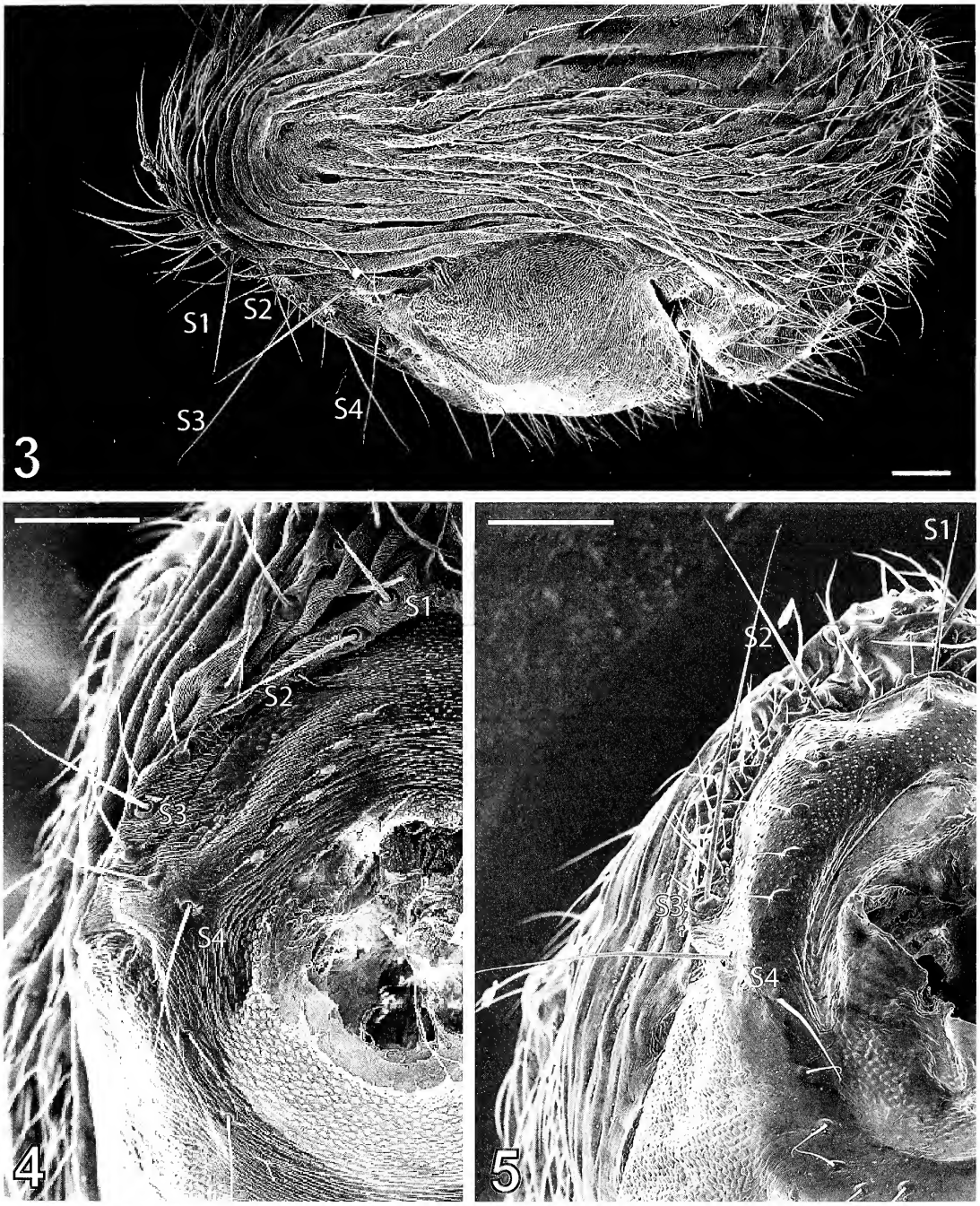


Figure 2.—Known EPS distribution plotted on a qualitative cladogram of spiders, used here to emphasize the overall distribution and scarcity of knowledge of EPS. Stars indicate presence, circles absence, question marks uncertainty.

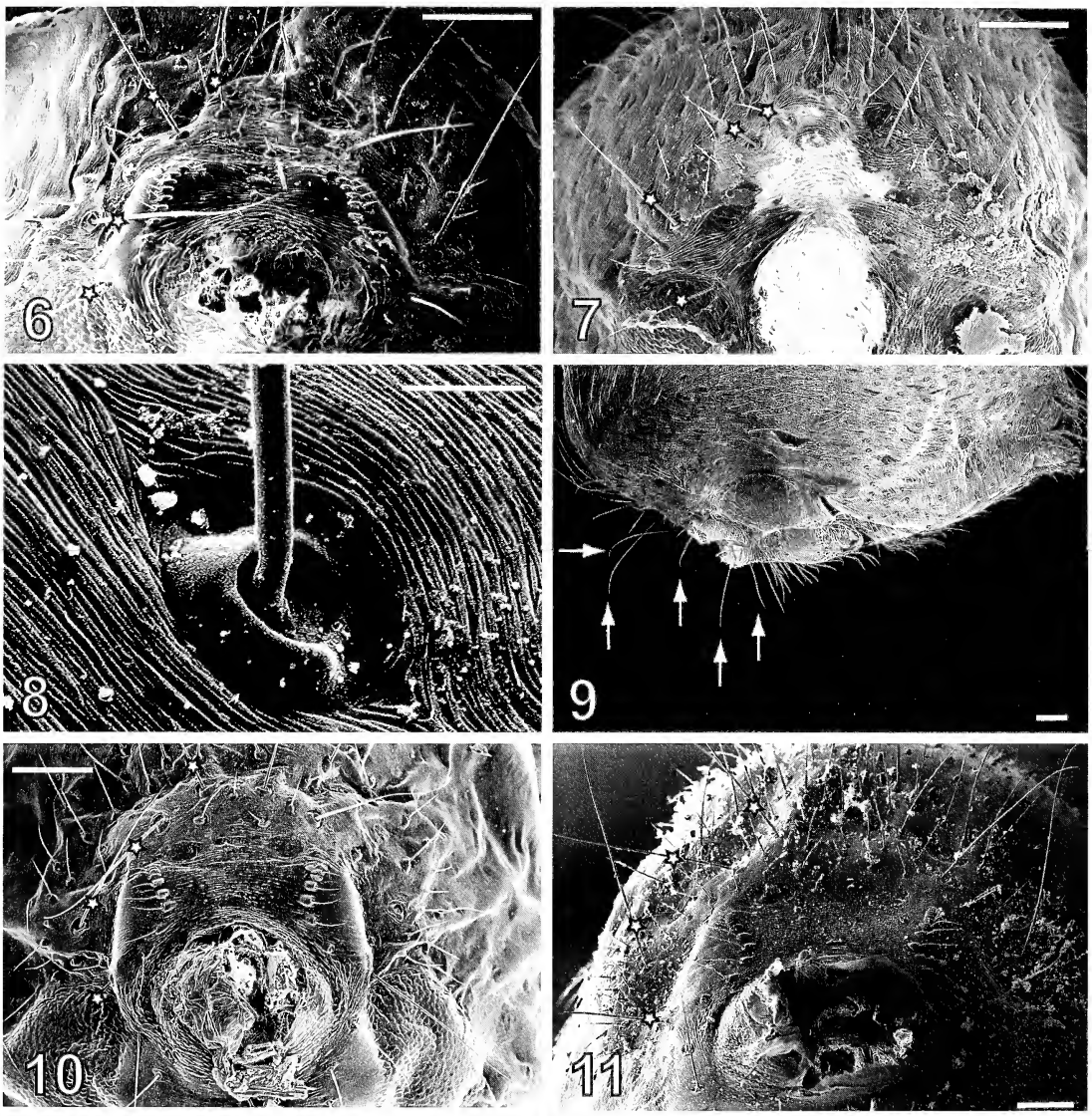
pothesis that EPS supplement the slit sensilla that also detect the relative position of the abdomen (Juberthie & Lopez 1994; Foelix 1996). Similarly, sensory setae at leg joints detect flexion when the setae press against adjacent body parts or the substrate and signal the movement and relative position of segments (Seyfarth 1985; Barth 2001), however, sensory setae on the abdomen are much less well known. Foelix (1979) may have been the first to speculate that particular abdominal setae were proprioceptive in spiders, but he did so only in a brief figure legend illustrating stridulation in *Argyrodes* (fig. 193, p. 270), and without further discussion. Juberthie & Lopez (1994) also described stridulation in male *Argyrodes* (also present in other male theridiids) in which modified and distinctly raised setal bases on the abdomen rub against grooves on the cephalothorax. They suggested that the setae that arise from these bases were proprioceptive. This remains to be confirmed, but it seems unlikely that setal proprioception, unlike stridulation, would be sexually dimor-



Figures 3–5.—Theridiidae males. 3–4. *Kochiura rosea* (Nicolet 1849) male. 3. Abdomen ectal view, ventral side down. 4. Pedicel area. 5. *Chrysso* nr. *albomaculata*. S-numbers indicate allocation of setae to sectors (see Methods). Scale bars = 100 μm.

phic. Regardless, evidence beyond morphology is needed to test the hypothesis of proprioceptive function.

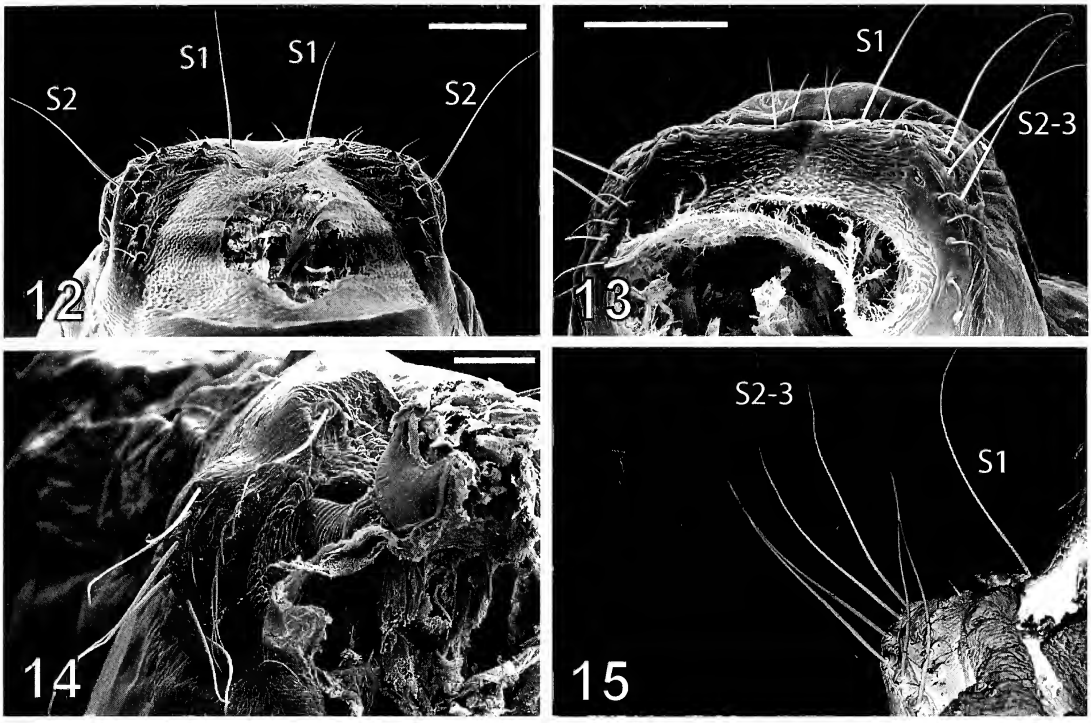
Given the phylogeny of Figure 2, basal araneomorphs (*Hypochilus* and *Austrochilus*) both have EPS in the relatively dorsal sectors 1 and 2. If present in haplogynes, they also tend to occupy sector 1, sometimes 2, and in *Scytodes* also 3. True palpimanoids, thus far, lack EPS. Non-orbicularian Entelegynae fre-



Figures 6–11.—*Anelosimus* (Theridiidae), stars and arrows indicate EPS. 6. *A. biglebowski* male. 7. *A. rupununi* Levi, 1956 female. 8. *A. biglebowski* male, detail of base of EPS setae. 9. *A. analyticus* male ectal view of abdomen with venter facing down. 10, 11. *A. studiosus* (Hentz 1850) males from Florida and Costa Rica, respectively. Scale bars: 6, 7, 9, 10 = 100 μm; 8 = 10 μm.

quently lack EPS and such presumably secondary losses may be informative. The 1-2-3 pattern is most frequent. Among orbicularians (treating *Mimetus* and *Textricella* as such), relatively basal orbicularians (deinopoids, araneids, nephilids, tetragnathids, symphytognathoids) tend to be 2-3 (also *Mimetus*), which may simply be the plesiomorphic 1-2 pattern displaced ventrally. Sheet-web weavers (Linyphiidae, Pimoidae, Synotaxidae, Cyatholipidae, Nesticidae, and Theridiidae) tend to have relatively more, and more ventral, EPS, e.g., 1-2-3-4 or 2-3-4.

None of these patterns may hold up. Observer error, especially in non-orbicularians, is probable. To confirm (or reject) the patterns reported here, verifying the presence of EPS in *Liphistius* and Mygalomorphae, and their absence in non-spider arachnids is a priority. However, proprioception at the pro/opisthosomal connection is *a priori* likely (see Lopez & Juberthie 1996), and certainly its mechanism



Figures 12–15.—Argyrodinae (Theridiidae) males, S-numbers indicate allocation of EPS to sectors (see Methods). 12. *Argyrodes argyrodes* (Walckenaer 1842). 13. *Rhomphaea metaltissima*. 14, 15. *Ariamnes attenuata*. Scale bars = 100 μm.

(EPS, slit sensilla, joint receptors) should be mapped and understood neurobiologically.

Several spider taxa seem to lack EPS (Fig. 37–44), although perhaps they are simply indistinguishable from normal abdominal setae, or greatly modified. In *Pardosa* sp. and *Gnaphosa parvula* Banks 1896 a brush of strong setae is located in sectors 1–2. These differ from typical proprioceptive setae in being stout and serrate, but they may be proprioceptive. Taxa without EPS probably indicate independent secondary losses of this sensory system rather than independent origins. Although patterns related to lifestyle in Table 1 appear weak, spiders do vary in the flexibility of their abdomens (aerial web spiders probably flex their abdomens more, and more precisely), and the patterns discussed above may reflect such differences.

In Theridiidae, EPS distribution defined generic and suprageneric taxa (Agnarsson 2004). Although the taxon sample here is quite sparse, intraspecific (Figs. 10, 11) and intrageneric variation seem low (Figs. 6–11) (see also Agnarsson 2004, characters 163–164; Agnarsson 2006, character 110). Related genera differ in the position and number of EPS. *Argyrodes* has one pair of EPS in sectors 1 and 2 (or 3), *Rhomphaea* has one pair in sector 1 and three pairs in sectors 2–3, and *Ariamnes* has one pair in sector 1 and at least six in sectors 2–3 (Figs. 12–15; generic patterns confirmed in an additional species of each genus, pers. obs.).

In summary, this is the first survey of a poorly known but complex, probably sensory system in spiders—elongated pedicillate setae—that appears to be a spider synapomorphy and useful for generic diagnoses and suprageneric phylogenetic reconstruction. The function of these setae should be investigated neurologically and behaviorally, and their patterns investigated among spiders and their relatives.

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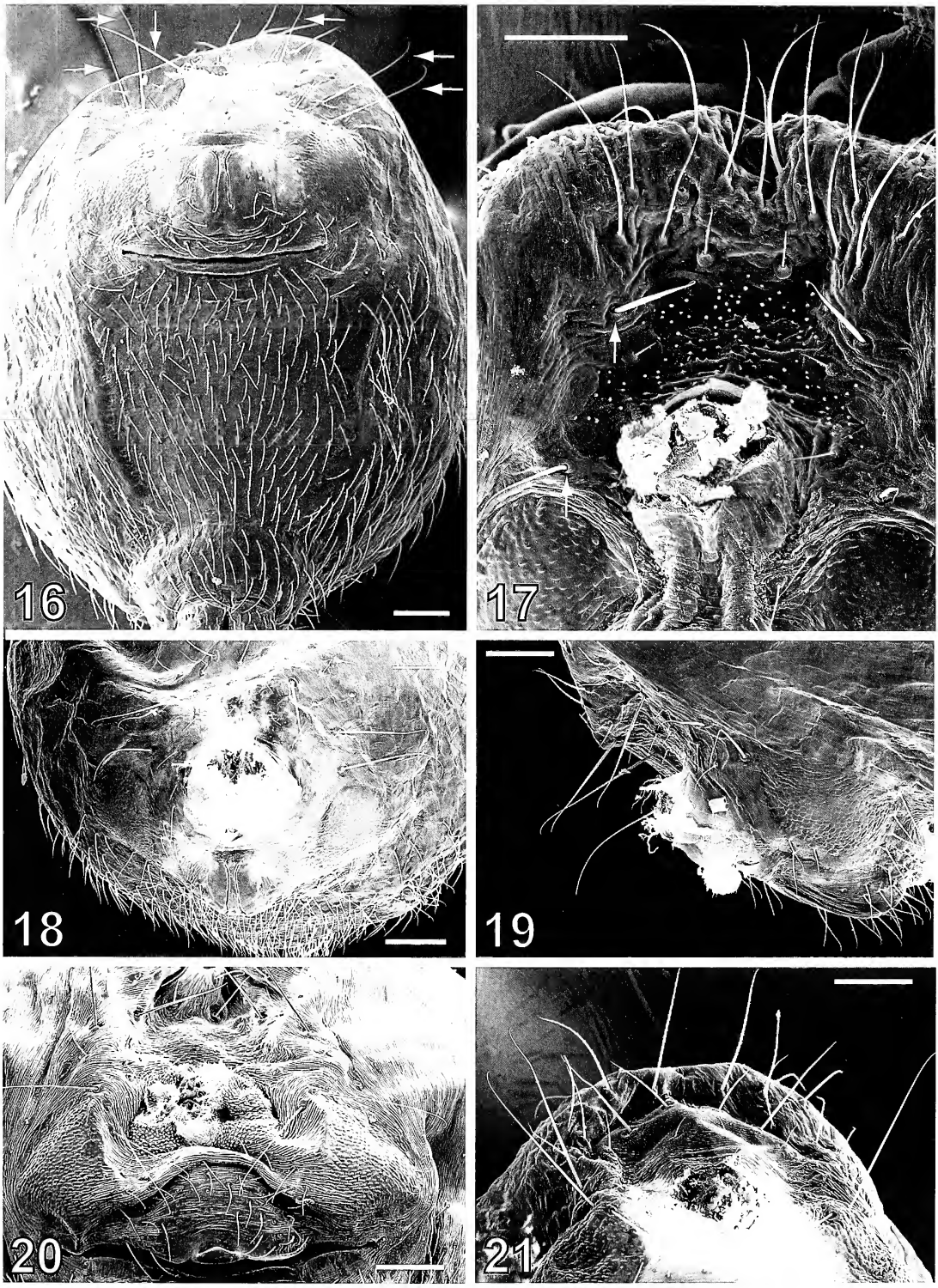
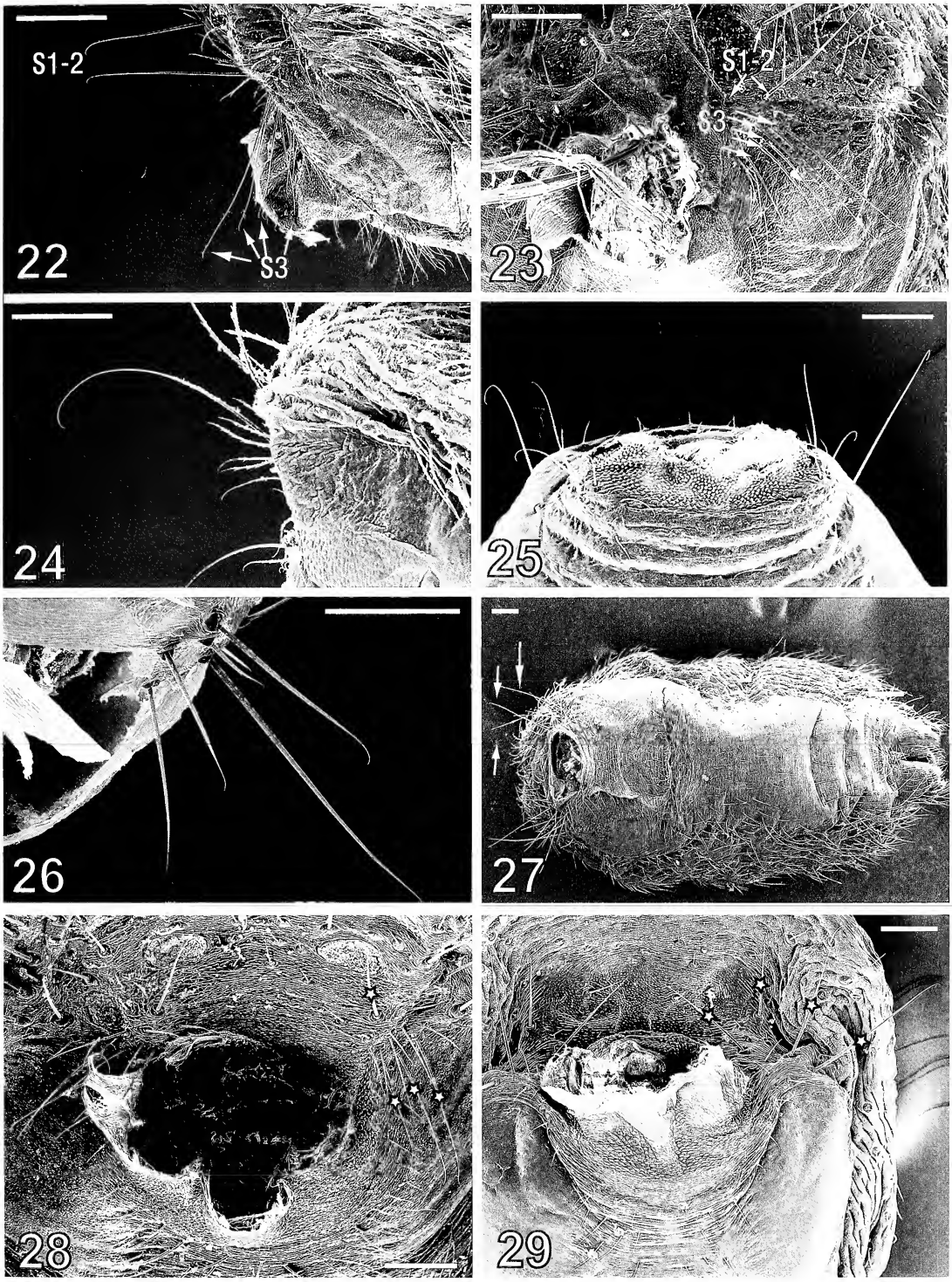
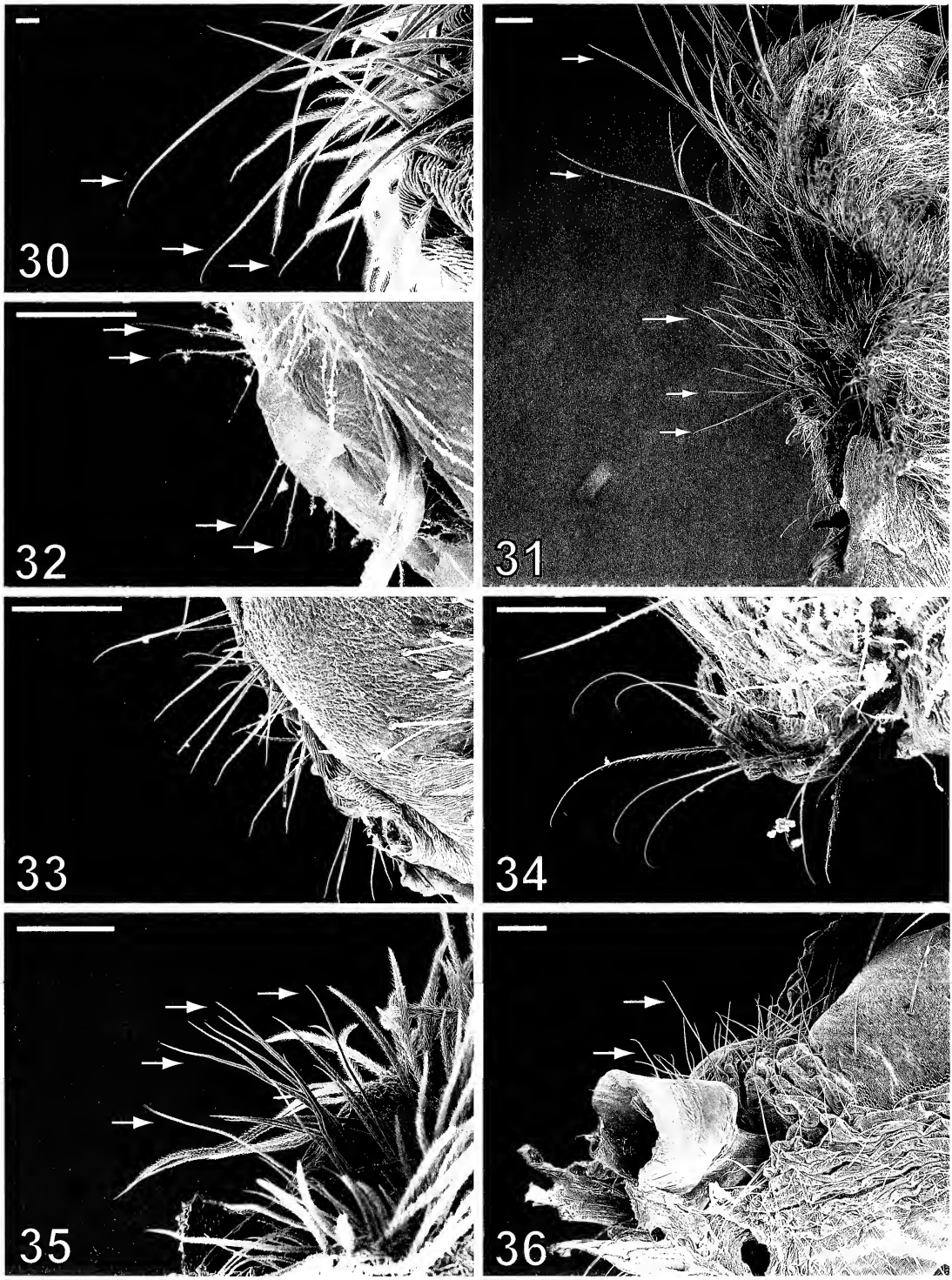


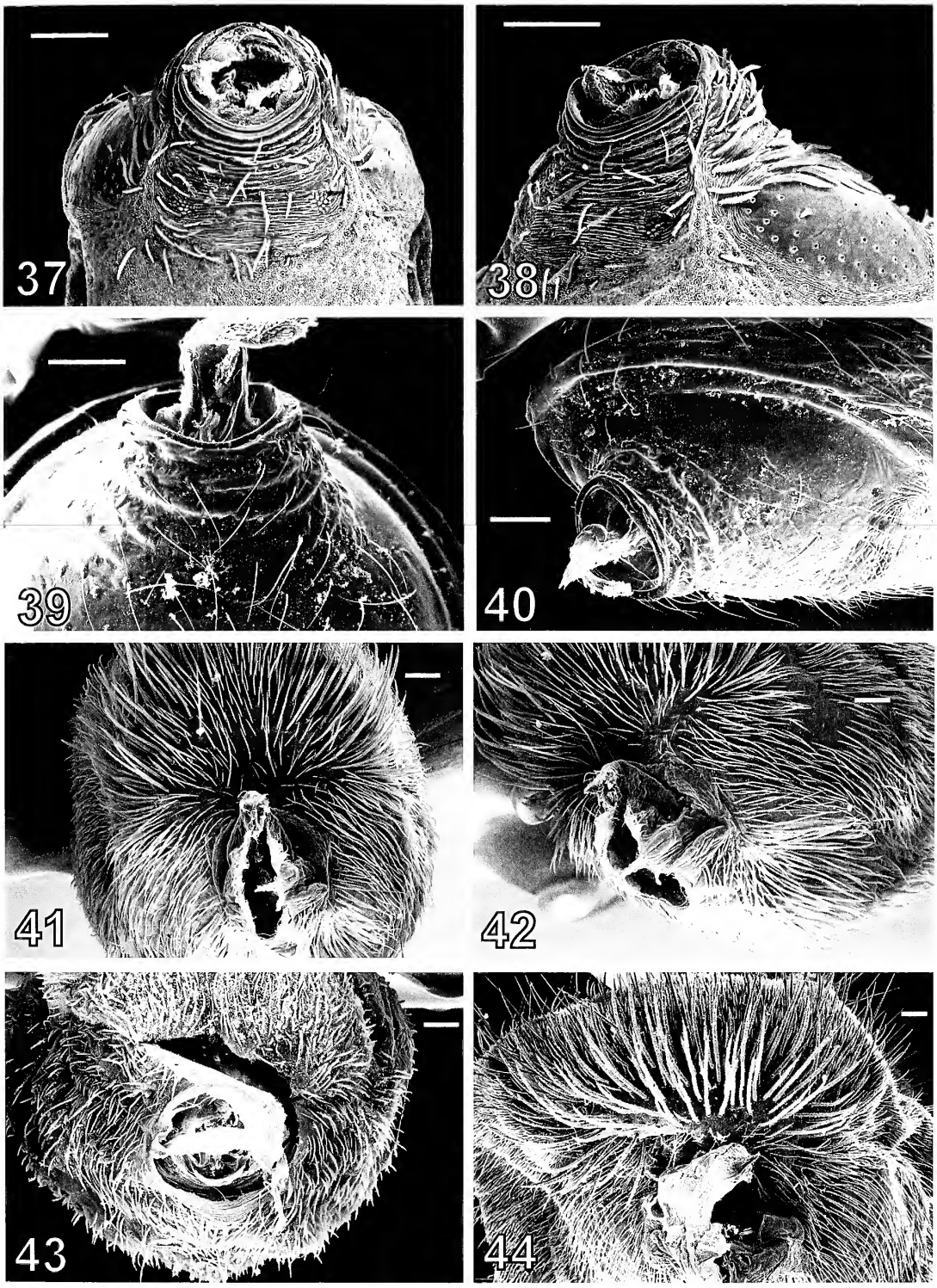
Figures 16–21.—Theridiidae females. 16, 18, 19, *Stemmops bicolor* O. Pickard-Cambridge 1894. 16. Abdomen ventral, arrows indicate EPS. 18. Area around pedicel, ventral view. 19. Area around pedicel, ectal view. 17. *Styposis selis*. Area around pedicel, ventral view. 20. *Selkirkiella magallanes* (Levi 1963). Area around pedicel and epigynum, ventral view. 21. *Selkirkiella* sp. Area around pedicel, ventral view. Scale bars = 100 μm.



Figures 22–29.—Orbiculariae males, stars and arrows indicate EPS and S-numbers their allocation to sectors (see Methods). 22, 23. *Pimoa breviata* (Pimoidae) male. 22. Ventral view. 23. Ectal view. 24. *Eidmanella pallida* (Nesticidae) male. Ectal view. 25. *Isicabu henriki* (Cyatholipidae). Ventral view. 26. *Mimetus interfector* (Mimetidae) male. Mesal view. 27. *Leucauge venusta* (Tetragnathidae) male abdomen. Ventral view. 28. *Nephila inaurata* (Nephilidae) male. 29. *Pronous tuberculifer* (Araneidae) male. Scale bars = 100 μm.



Figures 30–36.—Cribellate orbicularians and non-orbicularians, arrows indicate EPS. 30. *Deinopis* sp. (Deinopidae) male. 31. *Agelenopsis pennsylvanica* (Agelenidae) male. 32. *Oxyopes salticus* (Oxyopidae) male. 33. *Scytodes thoracica* (Scytodidae) male, with multiple EPS. 34. *Loxosceles deserta* (Sicariidae), male with a brush of bent-tipped EPS around the pedicel. 35. *Kukulcania hibernalis* (Filistatidae) male. Note that non-EPS abdominal setae are serrate or plumose (feathery). 36. *Hypochilus pococki* (Hypochilidae) male. Scale bars = 100 μm.



Figures 37–44.—Taxa where the EPS are clearly (37–40) or ambiguously absent (41–44). 37, 38. *Eriauchenius vadoni* (Archaeidae) male. 37. Ventral view. 38. Ectal view. 39, 40. *Chilenodes australis* (Malkaridae) male. 39. Ventral view. 40. Ectal view. Note that both *Archaea* and *Chilenodes* have modified (elongated) pedicels. 41, 42. *Pardosa* sp. (Lycosidae) male. 41. Ventral view. 42. Subectal view. 43. *Dictyna major* (Dictynidae) male. Ventral view. 44. *Gnaphosa parvula* (Gnaphosidae) male. Ventral view. Scale bars = 100 μm.

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A NEW SPECIES OF *TROGLOHYPHANTES* (ARANEAE, LINYPHIIDAE) FROM THE WESTERN ITALIAN ALPS

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ABSTRACT. *Troglohyphantes bornensis,* a new species from the western Italian Alps, is here described. According to the features of the male palp and female epigynum the new species can be assigned to Fage's III Group, Deeleman-Reinhold's *marqueti* group and Pesarini's *microcymbium* complex. All specimens were collected in the stony debris of Pugnetto caves (province of Turin, Italy), a calcschist cave complex, formerly studied by biospeleologists for the presence of several endemic species. All caves have openings into beech woods at an elevation of approximately 800 m.

RIASSUNTO. Viene descritta *Troglohyphantes bornensis,* una nuova specie delle Alpi occidentali italiane. A partire dalle caratteristiche del palpo del maschio e dell'epigino della femmina, la specie viene assegnata al III gruppo di Fage, al gruppo *marqueti* secondo Deeleman-Reinhold e, secondo Pesarini, al complesso *microcymbium*. Tutti gli esemplari provengono dal detrito delle Grotte del Pugnetto (Provincia di Torino, Italia), un sistema di grotte impostato in calcescisto, già noto per la presenza di numerose specie endemiche. Tutte le grotte si aprono ad una quota di 800 m circa, in boschi di faggio.

Keywords: *Troglohyphantes bornensis*, taxonomy, morphology, Europe, endemic distribution

In Italy the linyphiid spider genus *Troglohyphantes* Joseph 1881 is represented by 35 species distributed all over the Italian alpine range. One of these species (*T. excavatus* Fage 1919) is known from the Trieste Karst and two others (*T. delmastroi* Pesarini 2001 and *T. julianae* Brignoli 1971) are found in the Northern part of the Apennine range. The known distribution of *Troglohyphantes* species is often confined to very restricted areas and several species are recorded from just one or a few localities. Knowledge of the genus has grown considerably in the last 20 years with 14 new species described since 1987, especially thanks to the work of Carlo Pesarini (1988a, 1988b, 1989, 2001).

For several years we have been collecting data on the Italian species of *Troglohyphantes* to study their distribution and their phylogenetic development. A few specimens examined in this context have been assigned to a new species, *Troglohyphantes bornensis*, here described.

METHODS

The specimens are stored in 75% ethanol at the Museo Civico di Scienze Naturali "E. Caffi", Bergamo,Italy (MCSN), and studied using a Wild M8 stereoscopic binocular microscope. Illustrations were made using a camera lucida. All measurements are in mm. The following anatomical abbreviations are used in the text: ALE = anterior lateral eyes; AME = anterior median eyes; PLE = posterior lateral eye; PME = posterior median eye; total leg length; TmI = position of first metatarsal trichobothrium.

TAXONOMY

Family Linyphiidae Blackwall 1859
Genus *Troglohyphantes* Joseph 1881

Type species.—*Troglohyphantes polyophthalmus* Joseph 1881 by original designation.

Remarks.—The linyphiid spider genus *Troglohyphantes* is currently represented by 124 species, predominantly distributed in the European mountain ranges: Cantabric Mountains, Pyrenees, Alps, Carpathians, and Balkans. Moreover, four species are found in Northern Africa, two in Turkey, one in Iran, three in the Caucasus and one in the Canary Islands. Spiders belonging to this genus are found in a variety of habitats: caves, humus and rocks, moist and shaded situations. For the general description of the genus and for further information on autoecology refer to Fage (1919) and Deeleman- Rehinold (1978).

Troglohyphantes bornensis new species
Figs. 1–8

Material examined.—ITALY: *Piemonte*: Torino, Mezzenile: Holotype male, Cave "Borna Maggiore del Pugnetto," 810 m, 8 April 2006, M. Isaia (MCSN). Paratypes: 1 male, 1 female, same location as holotype, 7 July 1980, P.M. Giachino (MCSN); 1 female, same location as holotype, 1 April 2006, M. Isaia (MCSN); 1 female, same location as holotype, 17 June 2006, M. Isaia & R. Galindo (MCSN); 1 female, same location as holotype, 7 October 2006, M. Isaia (MCSN); 2 females, Cave "Borna Inferiore del Pugnetto," 810 m, 16 June 2006, M. Isaia (MCSN); 2 females, Cave "Borna Superiore del Pugnetto," 872 m, 1 December 2006, M. Isaia (MCSN); 1 female, Cave "Tana della Volpe," 885 m, 1 December 2006, M. Isaia (MCSN).

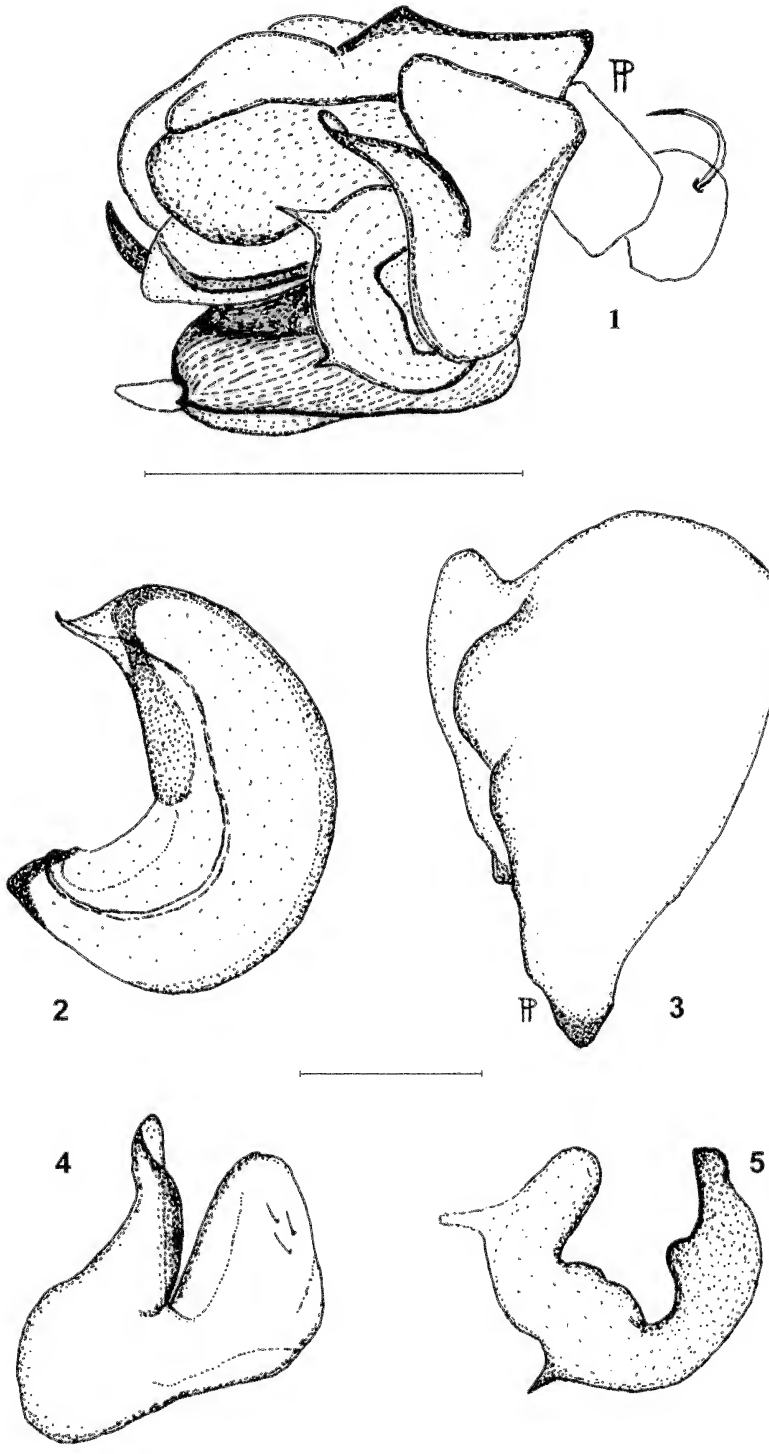
Etymology.—The species epithet is derived from "*borna*." In Alpine Provençal (spoken in several areas of the western Italian Alps) this term denotes a lair or a cave.

Diagnosis.—*Troglohyphantes bornensis* can be primarily distinguished from all other species of *Troglohyphantes* by the shape of lamella characteristica of the male. The shape of the female epigynum, as well as the suprategular apophysis and cymbium of the male are also diagnostic. The lamella characteristica consists of a simple lamellar, rounded lobe directed posteriorly and armed with two short tooth-shaped tips, the lower nearly orthogonal to the profile of the lamella and the upper, less spiky but longer, directed anteriorly, nearly parallel to the lower branch of the paracymbium. The male cymbium is smooth, the profile is not rounded, and it ends in a retro-lateral sub-apical lobe, directed proximally. The suprategular apophysis (Deeleman-Reinhold's "median apophysis") is directed upwards, nearly orthogonally, with a sharp end. The female epigynum is strongly protuberant with a short scape, is wider than long, and barely arched in lateral view.

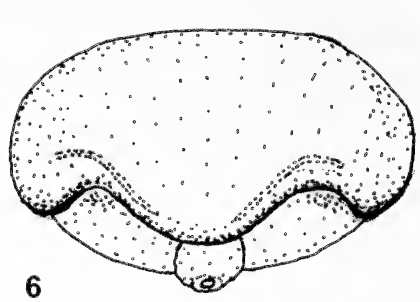
Description.—*Male (holotype)*: prosoma 1.19 long, 1.06 wide, yellowish. Anterior part of prosoma darker, tending to brown. Thoracic region rounded, dorsally with a narrow ridge, marked with a dark longitudinal streak. Eye region slightly elevated with a few black bristles encircling the eye group. Clypeus slightly indented under the eyes then convex. Eyes small but normally developed, surrounded by dark rings. AME smallest and very close to one another, PLE slightly bigger than PME, ALE slightly larger than PME, ALE and PLE contiguous. PLE–PME distance = 0.080, ALE–AME distance = 0.083, PME–PME distance = 0.083, AME–AME distance = 0.020. Eye diameters: AME 0.022, PME 0.037, ALE 0.048, PLE 0.050. Inter-ocular space with dark hairs, sometimes as long as clypeus. Sternum heart-shaped, yellowish with anterior edges darkened. Chelicerae brownish armed with three conspicuous anterior teeth and furnished with stridulating ridges on the retro-lateral portion. Legs medium-long (femur twice as long as the prosoma), uniformly yellowish. Leg I: femur 2.32, patella 0.39, tibia (absent), metatarsus (absent), tarsus (absent); leg II: femur 2.09, patella 0.44, tibia 2.24, metatarsus 2.06, tarsus 1.12, total leg length 7.95; leg III: femur 1.8, patella 0.37, tibia 1.71, metatarsus 1.64, tarsus 0.88, total leg length 6.4; leg IV: femur 2.19, patella 0.35, tibia 2.34, metatarsus 2.12, tarsus 1.0, total leg length 7.99. Abdomen 1.41 long, 0.88 wide, whitish-grey with dark hair. Male palp (Figs. 1–5): cymbium faintly convex, with two prolateral lobes and one central small protuberance with rounded profile ending proximally in a single apophysis, proximo-mesal part simple and truncated without protrusions or ridges. Superior branch of paracymbium sub-triangular, inferior branch dimly longer than the latter and distally bent nearly at a right angle, gradually narrowed anteriorly. Lamella characteristica with two short tooth-shaped tips, the lower nearly orthogonal to the profile of the lamella and the upper, less spiky but longer, directed upwards, nearly parallel to the lower branch of the paracymbium. Lamella ending in a rounded lobe directed backwards. Suprategular apophysis headed upwards, nearly orthogonally, with a sharp end. Tip of the embolus spiky tubular.

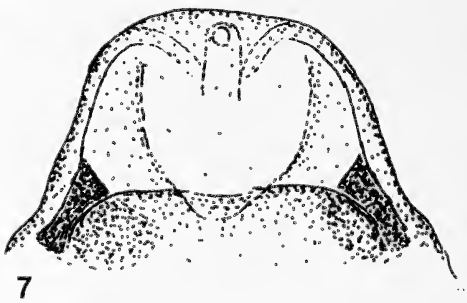
Female (paratype from "Borna Inferiore del Pugnetto"): prosoma 1.20 long, 1.06 wide, convex, smooth and slightly brighter than male. Thoracic region, ocular area, clypeus, sternum and chelicerae analogous to male in all features. PLE–PME distance = 0.046, ALE–AME distance = 0.063, PME–PME distance = 0.057. Eye diameters: AME 0.050, PME 0.065, ALE 0.078, PLE 0.052. Abdomen 2.13 long, 1.41 wide, whitish-grey with dark hairs. Patella of the palp armed with a dorsal noticeable spine, tibia with three long spines (one dorsal and two prolateral) and metatarsus armed with nine smaller spines of which two dorsal proximal, three prolateral, two retrolateral and two ventral apical. Leg I: femur 2.23, patella 0.39, tibia 2.38, metatarsus 2.04, tarsus 1.34, total leg length 8.38; leg II: femur 2.11, patella 0.42, tibia 2.21, metatarsus 1.87, tarsus 1.16, total leg length 7.77; leg III: femur 1.77, patella 0.35, tibia 1.67, metatarsus 1.52, tarsus 0.86, total leg length 6.17; leg IV: femur 2.28, patella 0.34, tibia 2.32, metatarsus 2.02, tarsus 1.07, total leg length 8.03. Epigynum (Figs. 6–8) strongly protuberant. Scape short, wider than long, U-shaped with two lateral incisions not pronounced and scarcely arched in lateral view.

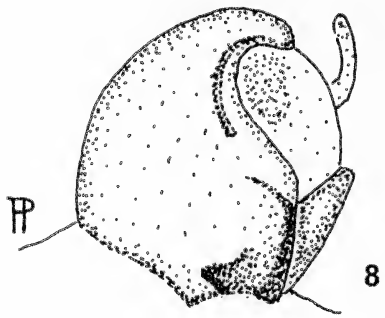
Spinal formulae: Male and female: femur I with one dorsal, one prolateral spine; femur II and III with one dorsal spine. Patella I–IV with one dorsal spine. Tibia I with two dorsal, one prolateral, one retrolateral spine; tibia II with two dorsal, one retrolateral spine, tibia III and IV with two dorsal spines. Metatarsus I–IV with one dorsal and one prolateral spine. Position of TmI: 0.2. Trichobothrium on metatarsus IV absent.



Figures 1–5.—*Troglohyphantes bornensis*, new species, male holotype: 1. Left male palp, retrolateral view; 2. Embolus, ventral view; 3. Cymbium, dorsal view; 4. Paracymbium, retrolateral view; 5. Lamella characteristica, retrolateral view. Scale lines = 0.5 mm (Fig. 1), 0.2 mm (Figs. 2-5).







Figures 6–8.—*Troglohyphantes bornensis*, new species, female paratype from Borna Inferiore del Pugnetto: 6. Epigynum, ventral view; 7. Epigynum, dorsal view; 8. Epigynum, lateral view. Scale line = 1 mm.

Distribution.—This species is confined to four caves situated in the Pugnetto region of the Western Alps.

DISCUSSION

Several authors have created species-groups within the genus *Troglohyphantes*. Fage (1919) proposed the first grouping and allocated the 13 species then known into four groups: I, II, III, and IV. Later Deeleman-Rehinold (1978) proposed a revision of the genus, grouping the species according to the shape of the epyginum into three series (A, B, and C) each with several groups. In a recent study on the Italian fauna, Pesarini (2001) allocated the 35 Italian species into 11 "complexes" that partially overlapped Deeleman-Reinhold's groups.

Several features suggest that *T. bornensis* belongs to Fage's III and Deeleman-Reinhold's *marqueti* group (series A): 1, shape of the male cymbium (proximo-mesal part simple and truncated without protrusions or ridges); 2, absence of Deeleman-Reinhold's "pocket" on the male paracymbium; 3, structure of lamella characteristica, with external and internal branch of the same length, internal branch without apophysis; 4, tip of male embolus acuminate; 5, epigynum not much incised posteriorly, scape wider than long.

Following the features utilized by Pesarini (2001), *T. bornensis* belongs to the *microcymbium* complex, a group that shows some similarities with Deeleman-Reinhold's *marqueti* group. Typical features of this complex are the shape of the male cymbium (roughly triangular and ending proximally in a single apophysis) and the scape of the female epigynum (short and widened, not much incised posteriorly). Pesarini's *microcymbium* complex currently only includes *T. microcymbium* (Pesarini 2001), an eyeless species known from a single locality in the Central Southern Alps. According to Pesarini (2001) himself, this species exhibits several features, such as the shape of the epigynum and cymbium, of Deeleman-Reinhold's *marqueti* group. Differences between *T. bornensis* and *T. microcymbium* are found in the dimensions of the male palp, the shape of the lamella characteristica, the presence of eyes, and the darker tegument.

The occurrence of a species belonging to the *marqueti* group in the Southern Alps is not surprising. The other species belonging to this group are found in the Cantabric mountains and Pyrenees, westerly, and in Istria and Anatolia, easterly. Nevertheless, Deeleman-Reinhold (1978) hypothesized that the origin of the *polyophtalmus* group (including numerous species from the Southern Alps) was from the *marqueti* group.

The composition of the various groups recognized within this genus is puzzling, especially concerning the Italian fauna. Since Deeleman-Rehinold (1978), 29 new species have been described, 18 of them from Italy. The partition into complexes by Pesarini (2001) only covers the Italian fauna and does not provide a complete diagnosis for each group. Therefore, as stated by the author himself, it cannot represent a helpful alternative to Deeleman-Reinhold's (1978) system. The collection of new data concerning the species, especially from the Southern Alpine area,

seems to be essential for a revision of the genus. According to several authors (see Fage 1919; Thaler 1967; Deeleman-Reinhold 1978; Brignoli 1979; Pesarini 2001), the importance of this genus is a crucial point in understanding the dynamics that lead to the origin of the current species assemblages in the Alpine area.

Biospeleological notes.—Specimens of *T. bornensis* have been found among stony debris in the four calcschist caves of the Pugnetto complex, in the vicinity of Mezzenile (40 km NW of Torino), at an elevation of approximately 800 m. All caves have openings into beech woods, with a prevalent northerly aspect to the cave opening. The temperature of the major cave ("Borna Maggiore del Pugnetto"), which is nearly 800 m in length, is consistently about 10°C. The three minor caves ("Borna Inferiore del Pugnetto," "Borna Superiore del Pugnetto," and "Tana della Volpe") are 64, 48 and 10 m in length respectively.

UTM ED50 coordinates for the caves are: Borna Maggiore del Pugnetto or Grotta del Pugnetto (Italian cadastrial number 1501Pi/TO) UTM 32TLQ3755675014637; Borna Inferiore del Pugnetto or Tana del Lupo (Italian cadastrial number 1502Pi/TO), UTM 32TLQ3753195014668; Borna Superiore del Pugnetto or Creusa d'le Tampe (Italian cadastrial number 1503Pi/TO) UTM 32TLQ3752725014453; Tana della Volpe (Italian cadastrial number 1504Pi/TO) UTM 32TLQ3752945014484.

The caves have been previously studied by several researchers (Capra 1924; Jeannel 1924, 1937; Capra & Conci 1931; Binaghi 1939; Arcangeli 1940; Casale 1980; Vailati 1988) and several interesting endemic species have been recognized, including *Alpioniscus feneriensis* (Parona 1880) (Isopoda, Trichoniscidae), *Dellabeffaella roccai* (Capra 1924) (Coleoptera, Cholevidae) and *Sphodropsis ghilianii* (Schaum 1858) (Coleoptera, Carabidae).

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THE SPIDER GENUS *DYSDERA* (ARANEAE, DYSDERIDAE) IN CENTRAL EUROPE: REVISION AND NATURAL HISTORY

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ABSTRACT. Nine species of the genus *Dysdera* were found to occur in central Europe: *D. adriatica* Kulczyński 1897, *D. crocata* Koch 1838, *D. dubrovninnii* Deeleman-Reinhold 1988, *D. erythrina* (Walckenaer 1802), *D. ninnii* Canestrini 1868, *D. hungarica* Kulczyński 1897, *D. lantosquensis* Simon 1882, *D. longirostris* Doblika 1853, and *D. taurica* Charitonov 1956. Two species, *D. dubrovninnii* and *D. lantosquensis*, are newly recorded from central Europe. The original description of *D. hombergi* (Scopoli 1763), the name used for a common species of the genus *Harpactea*, probably refers to *D. ninnii*. We retain the name *D. ninnii* as a *nomen protectum*. *Dysdera hamulata* Kulczyński 1897 appears to be a junior synonym of *D. maurusia* Thorell 1873. This North African species probably does not occur in central Europe, and a previous record from Slovakia is probably based on mislabeled material. A review of all species of *Dysdera* named from outside the Palearctic region demonstrated that *D. australiensis* Rainbow 1900 and *D. magna* Keyserling 1877 are junior synonyms of *D. crocata*, and that *D. bicolor* Tatzanovski 1874 and *D. solers* Walckenaer 1837 are erroneously placed in the genus *Dysdera*; the former is likely to be an oonopid and the latter a caponiid. In central Europe, *Dysdera* spiders prefer xerothermic forests, particularly sites enriched by calcium. All species probably have biennal life-cycles. The karyotype of males of seven species were examined, and diploid chromosome numbers were found to be extraordinarily variable, ranging from 9 (*D. crocata*) to 40 (*D. longirostris*). Karyotypes consist of holocentric chromosomes.

Keywords: Sibling species, karyotype, geographic parthenogenesis, taxonomy, thelytoky

Spiders of the genus *Dysdera* (Dysderidae) are ground dwellers characteristic of xerothermic forests of the Mediterranean and adjacent areas. During the day, they shelter in gravel covered by organic material or under stones, and at night they search for woodlice, their principal prey (Cooke 1965).

Comprising more than 240 species (Platnick 2007), *Dysdera* is currently the largest genus in the family Dysderidae and one of the richest Palearctic spider genera. Interestingly, the vast majority of species appear to be endemic to only small areas of the Mediterranean region, and only nine representatives appear to have colonized central Europe after the last glacial period. Although the species diversity in this region is low, there has been much confusion concerning their identification because of the uniformity in both the shape and body color, similarity in external female genitalic features and the presence of sibling species (e.g., Deeleman-Reinhold & Deeleman 1988).

A modern revision of the genus was initiated by Deeleman-Reinhold & Deeleman (1988), focusing on species from the eastern part of the Mediterranean. The genus was redefined and divided into different species-groups. This paper revises central European species of the genus *Dysdera*, based mainly on analysis of material from the Czech Republic and Slovakia. We solve some nomenclatural problems and summarize data on the distribution, habitat preferences, phenology and karyotypes of the species. We recognize eight species representing five groups within central Europe: *D. crocata* C.L. Koch 1838 (*crocata* group); *D. ninnii* Canestrini 1868, *D. dubrovninnii* Deeleman-Reinhold 1988 (*ninnii* group); *D. hungarica* Kulczyński 1897, *D. adriatica* Kulczyński 1897, *D. longirostris* Doblika 1853 (*longirostris*

group); *D. taurica* Charitonov 1956 (*lata* group); *D. erythrina* (Walckenaer 1802) and *D. lantosquensis* Simon 1882 (*erythrina* group).

MATERIAL AND METHODS

Distributional data and habitat preferences were obtained by analysis of extensive material from collections and during our field work. Selected localities were visited mainly in the summers of 1999–2005. Vegetation of inspected localities was characterized following Chytrý et al. (2001) and Moravec (1995).

Specimens were examined using a Nikon SMZ 645 stereomicroscope and an Olympus BX51 light microscope. Before examination, female vulvae were dissected and cleared in glycerol. The prosoma, chelicerae and bulbi of selected males were removed, placed on a stub, coated with gold and examined using a scanning electron microscope JEOL JSM 6400. To describe structures of the male pedipalp and the female vulva, we used the terminology of Arnedo et al. (2000).

Phenology was studied both on selected localities and by processing data on labels of the revised material. Phenological observations were performed on data from the following localities: Rokštejn [49°19′N, 15°43′E], Czech Republic (*D. ninnii*); Vinné near Michalovce [48°48′N, 21°58′E], Slovakia (*D. dubrovninnii*); Hrušov [48°36′N, 20°40′E] and Vinné near Michalovce, Slovakia (*D. hungarica*); Plitvička jezera [44°54′N, 15°36′E], Croatia (*D. adriatica*); Rilski monastir [42°07′N, 23°20′E] and Kranevo [43°20′N, 28°02′E], Bulgaria (*D. longirostris*); and Kranevo, Bulgaria (*D. taurica*).

For the karyological analyses, the most appropriate ontogenetic stage was found to be the adult male shortly after molting, which occurs at the end of the summer in all species studied. Testes at this stage contained numerous dividing cells suitable for karyotypic analysis, namely spermatogonial mitoses as well as various meiotic stages. The chromosome preparations were obtained by the method described in Pekár & Král (2001). Localities of karyotyped species were as follows: *D. crocata* – Kranevo near Varna, Bulgaria, 1 ♂; Çaytepe near Ordu, Turkey, 1 ♂; Mitra near Évora, Portugal, 4 ♂; Bloemfontein, South Africa, 1 ♂; Taborno, Tenerife, Spain, 2 ♂; *D. ninnii* – Rokštejn near Brtnice, Czech Republic, 2 ♂; *D. dubrovninnii* – Vinné near Michalovce, Slovakia, 2 ♂; *D. hungarica* – Hradisko near Hrušov, Slovakia, 2 ♂; *D. adriatica* – Korana near Plitvička jezera, Croatia, 1 ♂; *D. longirostris* – Kranevo near Varna, Bulgaria, 4 ♂; and *D. taurica* – Kranevo near Varna, Bulgaria, 2 ♂. Chromosome preparations were examined under immersion lens using an Olympus BX 50 light microscope.

Specimens are lodged in the following institutions: private collection of Aleš Jelínek, Telč, Czech Republic (AJ); Australian Museum, Sydney, Australia (AMS); Museum of Natural History, London, UK (BMNH); private collection of F. Gasparo, Trieste, Italy (FG); Magyar Természettudományi Múzeum, Budapest, Hungary (HNHM); private collection of J. Dolanský, Pardubice, Czech Republic (JD); private collection of J. Svatoň, Martin, Slovakia (JS); private collection of L. Kubcová, Prague, Czech Republic (LK); private collection of M. Antuš, Prague, Czech Republic (MA); Muséum d'Histoire Naturelle, Genève, Switzerland (MHNG); Muséum National d'Histoire Naturelle, Paris, France (MNHN); private collection of M. Řezáč, Prague, Czech Republic (MR); Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRS); Národní Muzeum, Prague, Czech Republic (NMPC); Naturhistorisches Museum, Vienna, Austria (NMW); private collection of P. Gajdoš, Nitra, Slovakia (PG); South Australian Museum, Adelaide, Australia (SAM); Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF); Univerza v Ljubljani, Slovenia (UL); Universidad de La Laguna, Spain (ULCI); private collection of V. Bryja, Brno, Czech Republic (VB); private collection of V. Hula, Brno, Czech Republic (VH); Vihorlatské múzeum, Humenné, Slovakia (VMH); private collection of V. Růžička, České Budějovice, Czech Republic (VR); Western Australian Museum, Perth, Australia (WAM); private collection of Z. Majkus, Ostrava, Czech Republic (ZM); Museum für Naturkunde, Humboldt Universität, Berlin, Germany (ZMHB).

TAXONOMY

Family Dysderidae C.L. Koch 1837
Genus *Dysdera* Latreille 1804

Type species.—*Dysdera erythrina* (Walckenaer 1802).

Remarks.—Comprising more than 240 named species (Platnick 2007), *Dysdera* is currently the largest genus in the family

Dysderidae. The vast majority of species appear to be endemic to the Mediterranean region; only nine representatives appear to have colonized central Europe.

KEY TO THE SPECIES OF CENTRAL EUROPEAN *DYSDERA*

1. Carapace smooth with rounded pits ..... 2 (*ninnii* group)
   Carapace wrinkled, without rounded pits 3
2. Cheliceral fang not flattened ..... *Dysdera ninnii*
   Cheliceral fang dorsoventrally flattened ..... *Dysdera dubrovninnii*
3. Tibiae III and IV with one or more dorsal spines ..... *Dysdera taurica* (*lata* group)
   Tibiae III and IV without dorsal spines 4
4. Femur IV with one or more dorsal spines ..... *Dysdera crocata* (*crocata* group)
   Femur IV without dorsal spines 5
5. Lateral anterior margins of carapace parallel (dorsal view), inner margin of basal cheliceral segment concave ..... 6 (*erythrina* group)
   Lateral anterior margins of carapace convergent (dorsal view), inner margin of basal cheliceral segment straight ..... 7 (*longirostris* group)
6. Mediodorsal margin of basal cheliceral segment concave, covered by short bristles; length of cheliceral fang/length of carapace more than 0.45; ventral side of tibia IV usually with three spines ..... *Dysdera lantosquensis*
   Mediodorsal margin of basal cheliceral segment convex, covered by normal hairs; length of cheliceral fang/length of carapace less than 0.45; ventral side of tibia IV usually with four spines ..... *Dysdera erythrina*
7. Ratio of the length of cheliceral fang and the length of carapace approximately 0.75 ..... *Dysdera longirostris*
   Ratio of the length of cheliceral fang and the length of carapace approximately 0.5 8
8. Male: bulbus with relatively parallel finger-like lateral sheet apophysis (Figs. 28, 29). Female: paired chitinized bands on the ventral wall of the copulatory bursa large and parallel (Fig. 30) ..... *Dysdera hungarica*
   Male: bulbus with relatively protruding finger-like lateral sheet apophysis (Figs. 32, 33). Female: paired chitinized bands on the ventral wall of the copulatory bursa narrow and anteriorly convergent (Fig. 34) ..... *Dysdera adriatica*

Dysdera crocata species-group

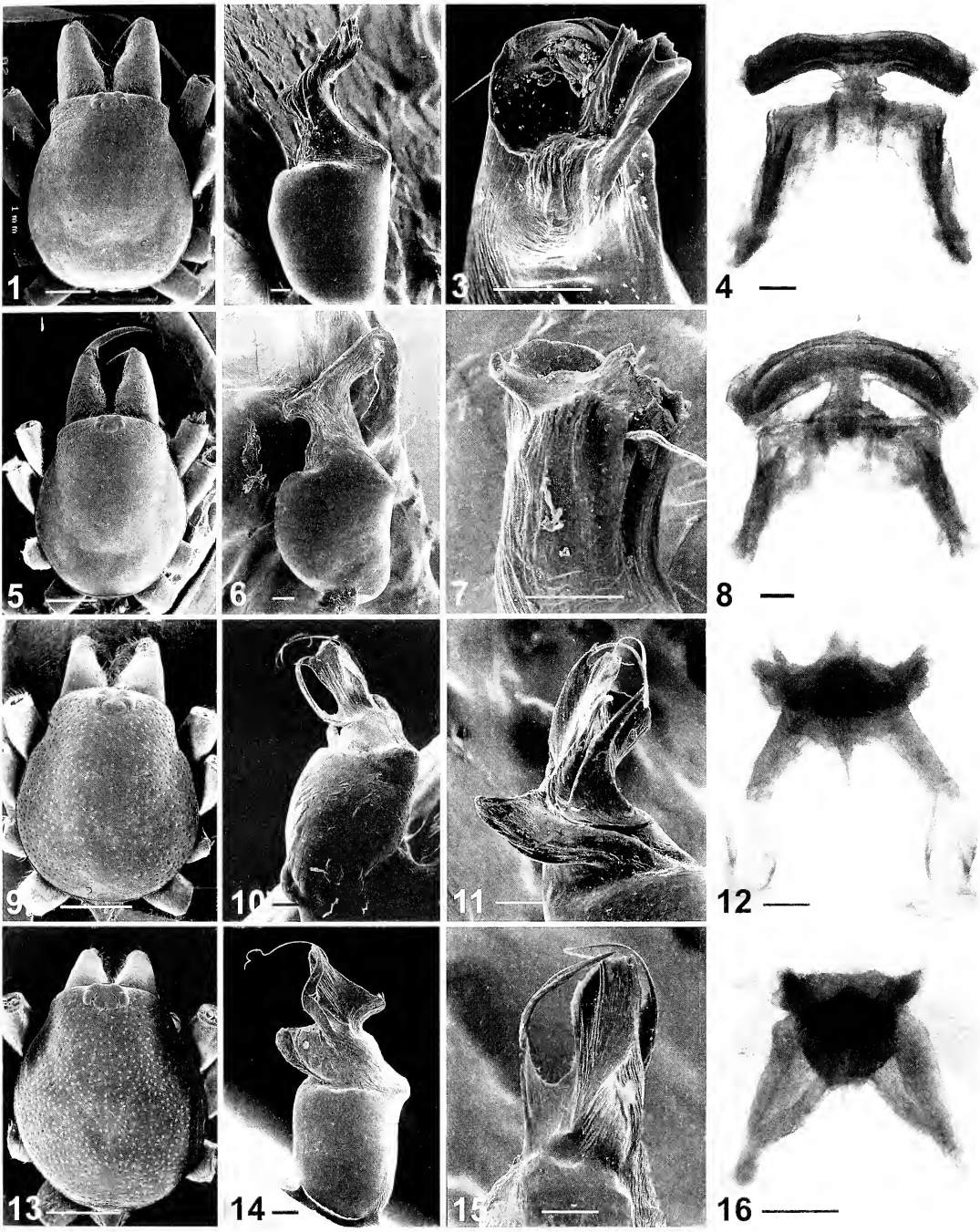
Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). Only one species of the group, *D. crocata* Koch 1838, has been found in central Europe. The other species, *D. hamulata* Kulczyński 1897 described from Slovakia (a junior synonym of *D. maurusia* Thorell 1873) probably does not occur in central Europe.

Dysdera crocata C.L. Koch 1838
Figs. 1–4, 17

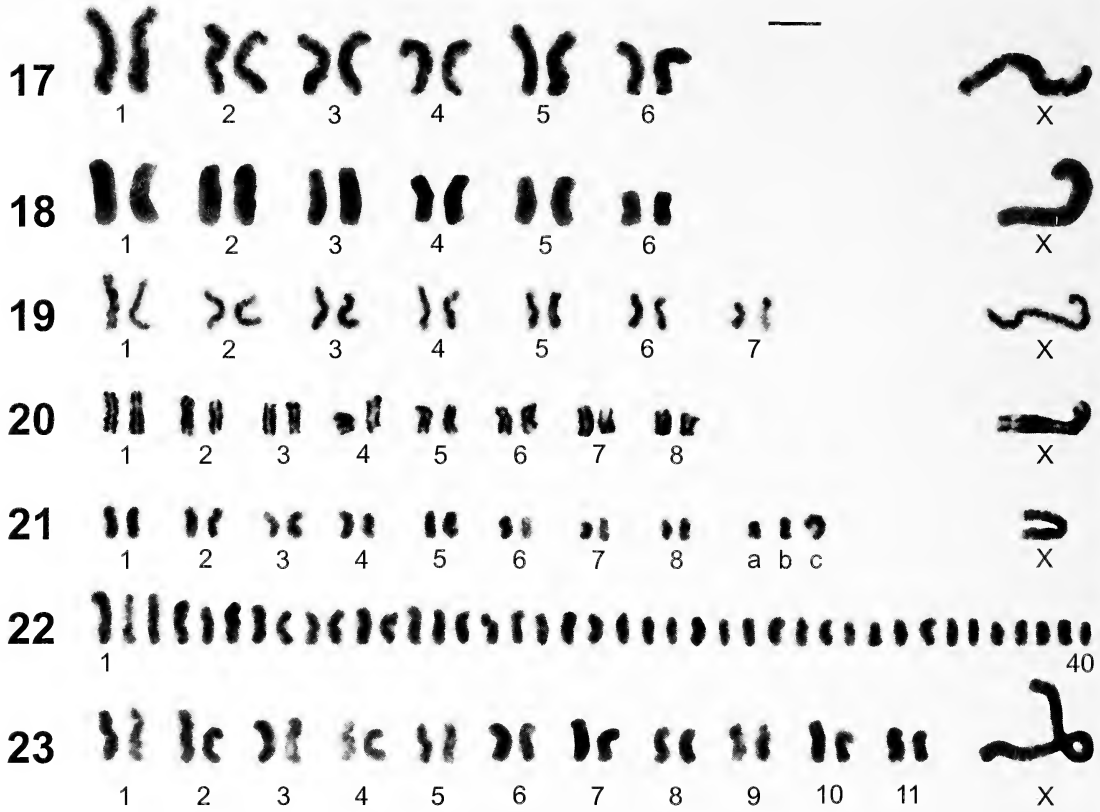
Dysdera crocata C.L. Koch 1838:81, figs. 392–394; Doblika 1853:119; Becker 1896:316, plate 17, fig. 21; Chyzer & Kulczyński 1897:268, plate 10, fig. 41; Bösenberg & Strand 1906:118, plate 16, fig. 445; Simon 1910:320, fig. 9K; Simon 1914:95, 111; Kaston 1948:62, figs. 7–10; Locket & Millidge 1951:84, figs. 41A, 42B–C, E; Wiehle 1953:19, figs. 44–48; Charitonov 1956:24, fig. 8; Grasshoff 1959:217, fig. 10; Cooke 1966:36, figs. 2, 4–6; Braendegaard 1966:71, figs. 59–61; Loksa 1969:78, figs. 54A–C; Tyschenko 1971:71, fig. 101; Cooke 1972:90, fig. 1; Dresco 1973:247, fig. 4; Roberts 1985:60, figs. 19b, d, f, h; Forster & Platnick 1985:214, figs. 831, 841, 860, 864; Yoshikura 1987:153, fig. 20.10A; Deeleman-Reinhold & Deeleman 1988:157, figs. 23–27; Heimer & Nentwig 1991:44, fig. 94; Wunderlich 1992:292, figs. 28–31; Dunin 1992:62, fig. 1; Roberts 1995:94; Wunderlich 1995:407, figs. 6–9; Dippenaar-Schoeman & Jocqué 1997: 155, figs. 73e, f; Mcheidze 1997:74, figs. 61–62; Roberts 1998:97; Song et al. 1999:68, figs. 27F–I; Arnedo et al. 2000:281, figs. 35, 37; Planet 1905:61, plate 4, fig. 1 (identification doubtful).

Dysdera interrita Hentz 1842:223; Emerton 1902:22, figs. 70–72; Comstock 1940:109, fig. 99.

Dysdera gracilis Nicolet 1849:340, plate 2, fig. 5.



Figures 1–16.—Characters of central European *Dysdera* species, *Dysdera crocata* and *D. ninnii* groups. 1–4. *Dysdera crocata*, male, from Mikulov, Czech Republic; female from Nieuwpoort, Netherlands; 5–8. *D. maurusia*, male from Beni Sauda, Algeria; female from Maison Carrée, Algeria; 9–12. *D. ninnii*, male and female from Brtnice, Czech Republic; 13–16. *D. dubrovninnii*, male and female from Michalovce, Slovakia: 1, 5, 9, 13. Male prosoma, dorsal view; 2, 6, 10, 14. Bulbus; 3, 7, 11, 15. Detail of distal division of bulbus; 4, 8, 12, 16. Anterior diverticle of vulva. Scale bars = 1 mm (prosomas), 0.1 mm (bulbi, vulvae).



Figures 17–23.—Male karyotypes: 17. *Dysdera crocata*; 18. *D. ninnii*; 19. *D. dubrovninnii*; 20. *D. hungarica*; 21. *D. adriatica*; 22. *D. longirostris*; 23. *D. taurica*. Karyotypes are based on spermatogonial metaphases. The numbers indicate autosome pairs except for the unresolved karyotype of *D. longirostris*, where they indicate particular chromosomes. Scale bar = 10 μm.

Dysdera rubicunda: Blackwall 1864a:371, plate 28, fig. 371; Menge 1872:297, plate 54, fig. 171.
Dysdera wollastoni Blackwall 1864b:179 (identification doubtful).
Dysdera balearica Thorell 1873:581 (identification doubtful).
Dysdera coerulescens Koch 1874:203 (identification doubtful).
Dysdera magna Keyserling 1877:230 [considered to be a synomym by Cooke (1967), however not accepted by Platnick (2007)]. **New synonymy.**
Dysdera maurusia: Dahl 1883:41.
Dysdera australiensis Rainbow 1900:485, plate 23, fig. 1 [considered to be a synomym by Cooke (1967), however not accepted by Platnick (2007)]. **New synonymy.**
Dysdera erythrina: Planet 1905:61, plate 4, fig. 2.
Dysdera sternalis Roewer 1928b:94.
Dysdera cretica Roewer 1928b:95, plate 1, fig. 1.
Dysdera menozzii Caporiacco 1937:58, fig. 1.
Dysdera palmensis Schmidt 1982:395, fig. 3.
Dysdera inaequuscapillata Wunderlich 1992:295, figs. 42–46.

Type material.—*Dysdera australiensis:* AUSTRALIA: *New South Wales:* female holotype, Sydney (33°52′S, 151°06′E) (AMS, examined).

Dysdera balearica: SPAIN: male holotype, Mallorca, Balearic Islands, F. Söderlund (repository unknown, not examined).

Dysdera coerulescens: GERMANY: syntypes: males and females, Lorsbacher near Nassau (50°23′N, 7°50′E), L. Koch, May 1871 (repository unknown, not examined); 1 specimen, same locality, O. Böttger, April 1873 (repository unknown, not examined).

Dysdera cretica: GREECE: juvenile holotype, Rethymnon (35°22′N, 24°28′E), Crete, C.F. Roewer, June 1926 (SMF, not examined).

Dysdera crocata: GREECE: syntypes: unknown number of adult specimens, Morea peninsula (37°30′N, 22°15′E), Peloponnesos, Schuh (perhaps BMNH, not examined).

Dysdera gracilis: CHILE: juvenile holotype, Santiago (33°28′S, 70°38′W) (repository unknown, not examined).

Dysdera inaequuscapillata: SPAIN: male holotype, Punta Hidalgo (28°31′N, 16°15′W), Tenerife, Canary Islands, 14 December 1986, R. Wis (ULCI, not examined). Paratypes: 1 male, 2 females, 1 juvenile, collected with holotype (ULCI, not examined); 1 female, same locality, 23 December 1986, C. Campos (ULCI, not examined); 1 male, Mercedes (28°31′N, 16°17′W), Tenerife, Canary Islands, Spain, May 1984, S. Morales (ULCI, not examined).

Dysdera interrita: USA: *Massachusetts*: syntypes: 1 male, 1 female, May, T.W. Harris (repository unknown, not examined).

Dysdera magna: BRAZIL: syntype: 1 female, Rio Grande do Sul (32°02′S, 52°06′W), (Uruguay is indicated in original description) (BMNH, examined).

Dysdera menozzii: LIBYA: syntypes: 3 males, 1 female, Tagiura (32°52′N, 13°21′E), C. Menozzio (repository unknown, not examined).

Dysdera palmensis: SPAIN: holotype female, Mazo (28°36′N, 17°45′W), La Palma, Canary Islands, G.E.W. Schidt (repository unknown, not examined).

Dysdera sternalis: GREECE: holotype female, Akrotiri, Crete, May 1926, C.F. Roewer (SMF, not examined).

Dysdera wollastoni: PORTUGAL: syntypes: 2 males, 3 females, 2 juveniles, Madeira (32°44′N, 16°59′W), T.V. Wollaston (repository unknown, not examined).

Other material examined.—ALGERIA: 1 ♂, M'sila area, Bou Saada [35°12′N, 4°10′E], (MNHN). AUSTRALIA: *Lord Howe Island* [31°33′S, 159°05′E]: 1 ♂, R. Baxter (AMS). *New South Wales:* 2 ♂, 4 ♀, Botany [33°56′S, 151°11′E], 1964–1965, 18 October 1978 (AMS); 1 ♂, 1 ♀, same location, 20 September 1966, R.E. Mascord (AMS); 1 ♂, 1 ♀, Sydney [33°52′S, 151°05′E], 22 April 1930, W.M. Pratt (AMS); 1 ♀, same location, 4 January 1955, A. Musgrave (AMS); 1 juvenile, North Sydney [33°44′S, 151°07′E], 4 June 1944, R. Virgona (AMS); 1 ♀, Mosman [33°49′S, 151°14′E], 29 November 1947, L.S. McKern (AMS); 1 ♀, Randwick [33°55′S, 151°14′E], 4 September 1951, T. Riding (AMS); 1 ♀, Moss Vale [34°33′S, 150°22′E], 2 October 1987, (AMS); 1 ♀, Northbridge [33°48′S, 151°13′E], 29 February 1972, J. Watson (AMS); 1 ♀, Mudgee [32°36′S, 149°34′E], 21 August 1989, J. McQuiggin (AMS); 1 ♀, Chippendale [33°53′S, 151°11′E], 11 February 1994, L. Bonsheck (AMS); 1 ♂, Forbes [33°23′S, 148°00′E], 16 September 1993, M.C. Daniel (AMS); 1 ♀, Pyrmont, Darling Island [33°51′S, 151°11′E], 6 December 1933 (AMS); 1 ♂, Pyrmont [33°52′S, 151°11′E], 1 February 2001, B. Dancs (AMS); 1 ♀, Surry Hills [33°53′S, 151°12′E], August 2001 (AMS); 1 ♂, East Lindfield [33°46′S, 151°11′E], 17 July 1956, D. MacMichael (AMS); 1 ♀, Bathurst [33°25′S, 149°34′E] (AMS); 1 juvenile, Clovelly [33°55′S, 151°15′E], 24 February 1944, R. Crapp (AMS); 1 ♂, 1 ♀, Enfield [33°53′S, 151°06′E], May 1949, L. Jarrett (AMS); 1 ♀, same location (AMS); 1 ♀, Canterbury [33°54′S, 151°07′E] (AMS); 1 ♀, Carlton [33°58′S, 151°08′E], July 1928, J. McClure (AMS); 1 ♀, Waverley [33°53′S, 151°15′E], B.W. Stevens (AMS); 1 ♂, Paddington [33°53′S, 151°13′E], 8 June 1971, P. Hutchings (AMS); 1 ♀, Kirribilli [33°50′S, 151°12′E], 1 August 1974 (AMS); 2 ♀, Kyeemagh [33°57′S, 151°09′E], October 1964, W.R. Macpherson (AMS); 1 ♂, 1 ♀, Rose Bay [33°52′S, 151°16′E], August 1963, A.L. Ironside (AMS); 1 ♂, Lakemba [33°55′S, 151°04′E], E.A. Brack (AMS). *Norfolk Island* [29°01′S, 168°02′E]: 1 ♀, 20 April 1993, H. Sampson (AMS); 1 ♂, 1 ♀ (AMS); 1 ♀, December 1915–January 1916, A.M. Lea (SAM). *Queensland:* 1 ♂, 1 ♀, Molangool W. [24°45′S, 151°32′E], H.H.B. Bradley (AMS, asigned as types of *Dysdera australiensis*). *South Australia:* 1 ♂, 1 ♀, Adelaide, Marino [35°02′S, 138°30′E], 10 August 1970, R.V. Southcott (SAM); 1 ♂, Adelaide [34°55′S, 138°35′E], 18 September 1911, G. Hilbig (SAM); 1 ♀, same location, 31 March 1976, R.V. Southcott (SAM); 1 ♀, same location, 26 August 1980, Cooter (SAM); 3 ♂, 2 ♀, 3 juveniles, Adelaide, Medindee [34°55′S, 138°35′E], 24 April 1989, Huilde (SAM); 1 ♀, Adelaide, Trinity Gardens [34°55′S, 138°35′E], 28 February 1987, D. Hirst (SAM); 1 ♀, Adelaide, Payneham [34°53′S, 138°37′E], 14 August 1967, R. Briggs (SAM); 1 juvenile,

Adelaide, Windsor Gardens [34°55′S, 138°35′E], 14 September 1991, D. Hirst (SAM); 1 ♀, Adelaide, Highgate [34°55′S, 138°35′E], October 1958, H.R. Lindsay (SAM). *Tasmania:* 3 ♂, 4 ♀, 3 juveniles, New Town [42°51′S, 147°17′E], 25 March 1939, March 1953, 16 March 1961, 27 October 1963, March 1965, V.V. Hickman AMS); 1 ♂, Risdon Rise [42°48′S, 147°21′E], 27 May 1929, V.V. Hickman (AMS); 2 ♀, Launceston [41°26′S, 147°08′E], 3 September 1929, V.V. Hickman (AMS); 2 ♂, Ulverstone [41°09′S, 146°10′E], 11 March 1992, A.F. Longbottom (WAM); 1 ♀, Davenport, the Forth river [41°10′S, 146°20′E], January 2003, M. Strnadová (MR). *Victoria:* 1 ♀, 3 juveniles, Balwyn [37°48′S, 145°05′E], 6 January 1982, 1 January 1983, M.S. Harvey (WAM); 1 ♂, 1 juvenile, Geelong [38°08′S, 144°20′E], 23 May 1978, R. Easton (WAM); 1 ♀, Melbourne, Ashburton [37°52′S, 145°04′E], 5 January 1988, P.K. Lillywhite (WAM); 2 juveniles, Wonthaggi [38°36′S, 145°35′E], 15 December 2002, M.S. Harvey (WAM); 1 ♀, Donvale [37°47′S, 145°11′E], 16 January 1983, M.B. Darby (WAM); 1 ♂, 1 juvenile, Surrey Hills [37°49′S, 145°05′E], 9 January 1982, M.S. Harvey (WAM); 1 ♀, Clayton [37°56′S, 145°08′E], 23 September 1982, B.E. Roberts (WAM). AUSTRIA: 1 ♀, Tyrol [47°15′N, 11°20′E] (BMNH). BELGIUM: 1 ♂, Nieuwpoort [51°07′N, 2°45′E], 30 April 2004, P. Saska (MR). CROATIA: 1 ♀, Senj (=Zeng) [44°59′N, 14°54′E], C. Chyzer (HNHM). CZECH REPUBLIC: 1 ♀, Prague [50°04′N, 14°26′E], 13 May 2001, Václavková (NMPC); 1 ♀, Mikulov [48°47′N, 16°37′E], 6 October 2002, J. Chytil (MR); 3 ♂, Brno, reserve Kavky [49°11′N, 16°36′E], 4 July 2005, 17 August 2005, S. Vinkler (VB). FRANCE: 1 ♂, Corsica [42°09′N, 9°04′E] (MNHN); 1 ♂, Banyuls [42°29′N, 3°07′E], 25 September 1962, L. Berland (MNHN); 1 ♂, Cerbère, Provence [42°26′N, 3°09′E] (BMNH). GREECE: 1 ♂, Leptokaria [40°03′N, 22°33′E], 4–13 June 1996, J. Dolanský (MR); 1 ♀, Chios island [38°23′N, 26°02′E], C.L. Koch (BMNH). IRELAND: 2 ♀, Dublin [53°20′N, 6°15′W], A.K.J. de Montmorency (BMNH). ITALY: 1 ♂, Naples [40°51′N, 14°16′E], Olf (ZMHB). PORTUGAL: 1 ♂, Algarve, Santa Bárbara de Nexe [37°06′N, 7°57′W], April 1963 (MNHN); 1 ♀, Mitra near Évora [38°33′N, 7°52′W], 1 November 2001, S. Pekár (MR). ROMANIA: 1 ♂, 1 ♀, Orşova [44°42′N, 22°23′E], Böckh (HNHM); 1 ♂, Costineşti [43°57′N, 28°37′E], 7–8 August, Dobnlu (NMPC). ?RUSSIA: 1 ♂, Caucasus (MNHN, *sub D. hungarica*). SLOVENIA: 1 ♀, Pridvor, Sv. Anton, Dekani, Koper [45°31′N, 13°50′E], August 1995, S. Toth (UL). SOUTH AFRICA: 1 ♂, 1 ♀, Bloemfontein [29°06′S, 26°13′E], 5 February 2005, M. Řezáč (MR). SPAIN: 1 ♀, unspecified location (ZMHB). *Minorca:* many ♂, ♀, unspecified location, D. Braun (BMNH); 2 ♂, 2 ♀, Mahon [39°53′N, 4°15′E], 28 December 1958, H. Coiffait (MNHN). *Tenerife:* 1 ♂, 1 ♀, Los Cristianos [28°03′N, 16°43′W], July 1972, I. Zunino (MNHN); 1 ♂, Anaga mountains, Taborno [28°32′N, 16°14′W], 2 March 2006, M. Řezáč (MR);1 ♂, Orotava valley, Aquamansa, La Caldera [28°20′N, 16°29′W], 7 March 2006, M. Řezáč (MR); 1 ♂, La Esperanza, Las rosas, Las Raices [28°26′N, 16°21′W], 8 March 2006, M. Řezáč (MR); 1 ♂, Labrada cave [28°27′N, 16°25′W], 17 March 2006, M. Řezáč (MR); 1 ♂, Icod de los Vinos, San Marcos [28°22′N, 16°42′W], 19 March 2006, M. Řezáč (MR). TUNISIA: 2 ♂, 2 ♀, unspecified location (NHRS); 2 ♀, Hammamet [36°24′N, 10°36′E], 7–20 May 1997, J. Dolanský (MR); 1 ♀, 1 juvenile, Zughonan [36°24′N, 10°08′E], 12 May 1997, J. Dolanský (MR); 1 ♂, 1 ♀, Kairanan [35°40′N, 10°05′E], April 1914 (MNHN). UKRAINE: *Crimea:* 2 ♂, 1 ♀, Cherson Taurica, Sevastopol [44°36′N, 33°31′E] (NHRS); 1 ♂, Yalta, Massandra Park [44°30′N, 34°11′E], 20 May–19 June 2001, N. Kovblyuk (MR); 1 ♂, Karadag, Beregovoy mountains [44°54′N, 33°36′E], 26 April 2003, N. Kovblyuk (MR). UNITED KINGDOM: 1 ♀, Box Hill, Surrey [51°23′N, 2°14′W], August 1989, M.R. Gray (AMS); 1 ♀, Worcestershire [52°17′N, 2°16′W] (AMS), 1 ♀, Brighton, Sussex [50°49′N, 0°08′W], 5 November 1933, A.F. Brazenor (BMNH); 1 ♀, Lewes, Sussex [50°52′N, 0°00′W], 3 May 1925, J.C. Campbell-Layor (BMNH); 1 ♀, London, Chiswick [51°29′N, 0°14′W], N.H. Benett (BMNH); 1 ♀, Weybridge [51°22′N, 0°27′W], D.Y. Burry (BMNH); 1 ♀, London, Acton [51°30′N, 0°16′W], 8 February 1944, W.E. Woodward (BMNH). U.S.A.: 1 ♀, Michigan, Ann Arbor [42°16′N, 83°43′W], April 1992, A. Richards (WAM). UZBEKISTAN: 1 ♀, Buchara [39°46′N, 64°25′E] (ZMHB).

Diagnosis.—This species is very similar to some species of the *crocata* group, which are

restricted to the southern part of Mediterranean region, mainly northern Africa, and require further taxonomic study. Among central European species it belongs to the largest one; it is characteristic by femur IV with one or more dorsal spines and by remarkably parallel lateral margins of cephalic part of carapace; the males are characteristic by inflexed distal division of the bulbus; the females are characteristic by proximally situated, wide, equally incurved spermatheca and by endogynal ventral arch with remarkable shoulders.

Description.—*Carapace* (Fig. 1): carapace 4.2–4.9 mm long, slightly wrinkled, ferruginous to orange, dorsoventrally flat. Lateral margins of cephalic part parallel. *Chelicerae* (Fig. 1): basal segment elongated (basal segment length/carapace length = 0.53), dorsally convex, slightly wrinkled, covered with piligerous granulations. Groove elongated (length of groove/basal segment length = 0.61), equipped with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Median cheliceral tooth close to basal cheliceral tooth. Fang elongated (fang length/carapace length = 0.51), thorn-shaped. *Legs:* femora I–III spineless, femora IV usually with 1–3 dorsal spines. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–2 additional spines. *Bulbus* (Figs. 2, 3): distal division narrower than tegulum, incurved, with pronounced posterior apophysis on flexion. Posterior apophysis not fused to tegulum. Arch-like ridge on apical part of bulbus without any apophysis. *Vulva* (Fig. 4): spermatheca proximally situated, wide, equally incurved. Dorsal arch rectangular. Neck connecting spermatheca with ventral wall of copulatory bursa with prominent frill in retroventral view. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—This species has been described several times under different names from various parts of the world. Cooke (1967) suggested that *Dysdera magna* Keyserling 1877, described from Brazil and reported also from Uruguay (Díaz & Sáez 1966) and *D. australiensis* Rainbow 1900 from Australia, are both junior synonyms of *D. crocata*. However, this synonymy was not definitive and not accepted [see Platnick (2007)]. We checked the genital morphology of the type specimens of these two species and found them to be morphologically identical with *D. crocata*. Furthermore, after examination of the relevant collections from Australian museums, we were unable to locate any species other than *D. crocata*. Díaz & Sáez (1966) reported a different chromosome number (2n ♂ = 9) from a population from Uruguay identified as *D. magna*. This population might represent a cryptic species introduced to South America together with *D. crocata*. The synonymies of *D. balearica* Thorell 1873 and *D. coerulescens* Koch 1874 with *D. crocata* are based on the conjectures published by Simon (1914). Even though they have never been accurately argued they are currently accepted (Platnick 2007). Both species were described after comparison with true *D. crocata* (Thorell 1873; Koch 1874). Unfortunately the deposition of the type material of these two species, necessary for conclusive confirmation or rejection of synonymy, is unknown. A female identified as *D. crocata* illustrated in Planet (1905) resembles *D. longirostris* due to the remarkably elongate chelicerae.

Karyotype.—Analysis of male meiotic division indicated the sex chromosome system X0 in all specimens. Remarkable variation was found in the number of autosomal pairs. Males from Bulgaria and South Africa exhibited four, those from Turkey five, and those from the Canary Islands and Portugal six autosomal pairs (Fig. 17).

Habitat.—In central Europe *D. crocata* occurs only in relatively dry, synanthropic, or semisynanthropic and adjacent habitats.

Distribution.—This species has been found on all continents except for Antarctica. In central Europe, its distribution is usually limited to urban areas. This species is new for the Czech Republic. Maps of occurence in other European countries can be found in Deltshev et al. (2003: map 15) (Serbia), Ribera et al. (1989: fig. 1) (Spain), Romano & Ferrández (1983: map 4) (Spain, province Navarra), Gajdoš et al. (1999: map 150) (Slovakia, partly based on misidentifications).

Dysdera maurusia Thorell 1873 status revised
Figs. 5–8

Dysdera maurusia Thorell 1873:467.

Dysdera crocota var. *hamulata* Kulczyński, in Chyzer & Kulczyński 1897:268, plate 10, fig. 41. **New synonymy.**

Dysdera hamulata: Simon 1914:112.

Dysdera crocata: Drensky 1938:92, fig. 8a.

? *Dysdera hamulata*: Deeleman-Reinhold & Deeleman 1988:160, fig. 23a, 24a. (misidentification).

Type specimens.—*Dysdera maurusia*: ALGERIA: syntypes: 1 male, 2 females, Alger, El Harrach (= Maison Carrée) (36°42′N, 3°07′E), H.A. Eurén (NHRS, examined).

Dysdera hamulata: SLOVAKIA: male holotype, Vranov nad Topľou (48°53′N, 21°41′E) (locality possibly in error, see below) (repository unknown, not examined).

Other material examined.—ALGERIA: 3 ♂, M'sila area, Bou Saada [35°12′N, 4°10′E] (MNHN); 1 ♂, unspecified location (MNHN); 1 ♂, Alger area, Kouba, Ravin de la Femme Sauvage [36°43′N, 3°04′E], December 1892, P. Lesne (MNHN); 1 ♂, Tlemcen [34°53′N, 1°18′W] (MNHN). USA: *New York*: 1 ♂, Poughkeepsie [41°42′N, 73°54′W], N. Banks (MNHN) (probably mislabeled, see below).

Diagnosis.—In contrast to the otherwise similar *D. crocata*, this species is smaller and the lateral margins of the cephalic part of carapace are not distinctly parallel; in males the arch-like ridge on the apical part of bulbus is elongated to a hook-shaped apophysis; in females the neck connecting the spermatheca with the ventral wall of the copulatory bursa is without a frill.

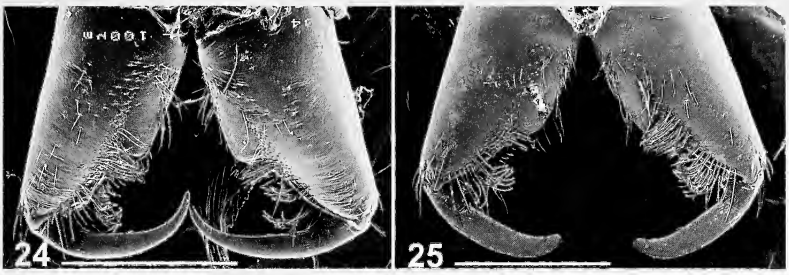
Description.—*Carapace* (Fig. 5): carapace 2.3–4.0 mm long, slightly wrinkled, ferruginous to orange, dorsoventrally flat. Lateral margins of cephalic part are slightly convergent. *Chelicerae* (Fig. 5): basal segment elongated (basal segment length/carapace length = 0.55), dorsally convex, slightly wrinkled, covered with piligerous granulations. Groove elongated (length of groove/basal segment length = 0.61), equipped with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Median cheliceral tooth close to basal cheliceral tooth. Fangs elongated (fang length/carapace length = 0.50), thorn-shaped. *Legs:* femora I–II spineless, femora III sometimes with 1, femora IV usually with 2–5 dorsal spines. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–2 additional spines. *Bulbus* (Figs. 6, 7): distal division narrower than tegulum, incurved, with pronounced posterior apophysis on its flexion. Posterior apophysis not fused to tegulum. Arch-like ridge in apical part of bulbus elongated to hook-shaped apophysis. *Vulva* (Fig. 8): spermatheca proximally situated, wide, equally incurved. Dorsal arch rectangular. Neck connecting spermatheca with ventral wall of copulatory bursa basally robust, without frill. For detailed description see Thorell (1873).

Remarks.—The original description of *D. maurusia* is insufficient, as it lacks any drawings (Thorell 1873). Simon (1914) synonymized it with *D. crocata* without examining the type material, and this synonymy is still accepted [see Platnick (2006)]. Thorell's syntypes comprise a single male and two females. Both females belong to the same species. Since the species diversity of *crocata* group in northern Algeria is enormous, the pairing of these females with the male is not definite. The male corresponds with the description of *D. hamulata* Kulczyński 1897. Moreover the apical portion of the bulbus is identical in every detail with the detailed drawing of *D. hamulata* in Chyzer & Kulczyński (1897). Therefore, we propose to remove *D. maurusia* from the synonymy with *D. crocata* and consider *D. hamulata* a junior synonym of *D. maurusia*.

The record of *D. hamulata* from Turkey (Deeleman-Reinhold & Deeleman 1988) is erroneous as the bulbus depicted suggests it belongs to *D. flagellata* Grasshoff 1959.

A drawing of *D. crocata* in Drensky (1938) is remarkably similar to *D. maurusia*; however, neither *D. maurusia* nor *D. crocata* was found in Drensky's collection (Ch. Deltshev, pers. comm.). His drawing is probably a compilation of fig. 41a (general shape of *D. crocata* bulbus) and 41d (detail of apical part of *D. crocata* var. *hamulata* bulbus) from Chyzer & Kulczyński (1897).

Distribution.—This species is known from northern Algeria. The record from Slovakia (Gajdoš et al. 1999) is based on the reference in Chyzer & Kulczyński (1897); we consider this record referring to a single male doubtful. This species has never been found again despite an intensive search all over Slovakia (*cf.* Gajdoš et al. 1999). Furthermore, we failed to find this species at the only locality mentioned in Chyzer & Kulczyński (1897), Vranov nad Topľou. It appears that the type material of *D. hamulata* was mislabeled. The drawing of this species in Drensky (1938) does not seem to be based on material from Bulgaria (see Remarks). The material labeled with an American locality (see Material examined) is probably also from north



Figures 24–25.—Chelicerae, ventral view. 24. *Dysdera ninnii*; 25. *D. dubrovninnii*. Scale bars = 1 mm.

Africa because it contains not only *D. maurusia* but also another species belonging to the *crocata* group, the species-group which is exclusively restricted to northern Africa and closely adjacent regions.

Dysdera ninnii species-group

Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). Two closely related representatives of this group have been found to occur in central Europe, *D. ninnii* Canestrini 1868 and *D. dubrovninnii* Deeleman-Reinhold 1988.

Dysdera ninnii Canestrini 1868
Figs. 9–12, 18, 24, 26

Aranea hombergi Scopoli 1763:403 (nomen dubium).

Dysdera ninnii Canestrini 1868:190; Canestrini & Pavesi 1868:845; Canestrini & Pavesi 1870:25, plate 3, fig. 2; Herman 1879:204–205; Chyzer & Kulczyński 1897:268, plate 10, fig. 44; Roewer 1928a:49, plate 7, fig. 561; Drensky 1938:93, fig. 8d (possibly compilation of figures from Chyzer & Kulczyński (1897) and Simon (1914)); Loksa 1969:74, figs. 49B, D, 50, 51A–B; Deeleman-Reinhold & Deeleman 1988:180, figs. 14, 16, 111–118; Heimer & Nentwig 1991:44, fig. 92; Thaler & Knoflach 2002:418, figs. 6–7; Pesarini 2001: figs. 7, 9, 11; Schult 1983:71, fig. 6 (misidentification); Simon 1914:95, 112, fig. 159 (doubtful).

Dysdera pavesii Thorell 1873:564 (doubtful).

Type specimens.—*Dysdera hombergi:* syntypes: SLOVENIA: unknown number of specimens, Carniola (repository unknown, not examined).

Dysdera ninnii: syntypes: ITALY: unknown number of males and females, regions Trentino, Veneto and Modenese (repository unknown, not examined).

Dysdera pavesii: syntypes: ITALY: males and females, G. Canestrini (repository unknown, not examined).

Material examined.—AUSTRIA: 1 ♀, unspecified location (NHRS). BOSNIA & HERCEGOVINA: 1 ♀, Visovica [43°59′N, 18°27′E], 22 June 1893, L. Gíró (HNHM). CROATIA: 1 ♂, 21 ♀, Velebit, Paklenica [44°19′N, 15°28′E], 18–21 June 2005, M. Řezáč (MR); 3 ♀, Šibenik, Solaris [43°44′N, 15°53′E], 16–17 June 2005, M. Řezáč (MR); 4 ♀, Plitvička jezera, Korana [44°54′N, 15°36′E], 22 June 2005, M. Řezáč (MR). CZECH REPUBLIC: *Tišnovsko area:* 1 ♀, Horní Čepí near Nedvědice [49°28′N, 16°20′E], 10 May, F. Miller (NMPC); 2 ♀, Doubravník [49°26′N, 16°22′E], 10 June 1983, F. Miller (NMPC). *Pálava biospheric reserve:* 1 ♀, Pouzdřany, reserve Pouzdřanská step-Kolby [48°56′N, 16°38′E], 1983, F. Miller (NMPC); 1 ♀, same location, 24 April–22 May 2005, S. Vinkler (VB). *Moravský kras area:* 1 ♂, 2 ♀, 1 juvenile, Blansko, Těchov, reserve Vývěry Punkvy, Skalní mlýn [49°23′N, 16°47′E], 21 May 1993, 31 May 1997–27 May 1998, V. Růžička (VR); 1 ♂, 2 ♀, Brno, reserve Kavky [49°11′N, 16°36′E], 18 May 2005, 18 October 2005, S. Vinkler (VB). *Jihlavské vrchy mountains:* 1 ♂, Brtnice, Přímělkov [49°21′N, 15°43′E], 8 June–11 July 1995, A. Jelínek (AJ); 1 ♀, Brtnice, Rokštejn ruin [49°19′N, 15°43′E], 26 May 1994, E. Svatoňová (JS). *Znojemská pahorkatina (hilly country):* 1 ♂, Mohelno, reserve Hadcová step [49°06′N, 16°10′E], 1 June 1983, F. Miller (NMPC); 3 ♂, 4 ♀, Vranov nad Dyjí, Braitava [48°53′N, 15°48′E], 9–24 May 1995, 15 May–5 June 1996, 28 August–18 September 1996, 18 September–9 October 1996, 9–30 October 1996, A. Reiter (VB); 1 ♀, 1 juvenile, Vranov nad Dyjí [48°53′N, 15°48′E] (NMPC). HUNGARY: 4 ♀, 1 juvenile, Misina hill above Pécs [46°05′N, 18°13′E], 30 September 2006, M. Řezáč (MR).

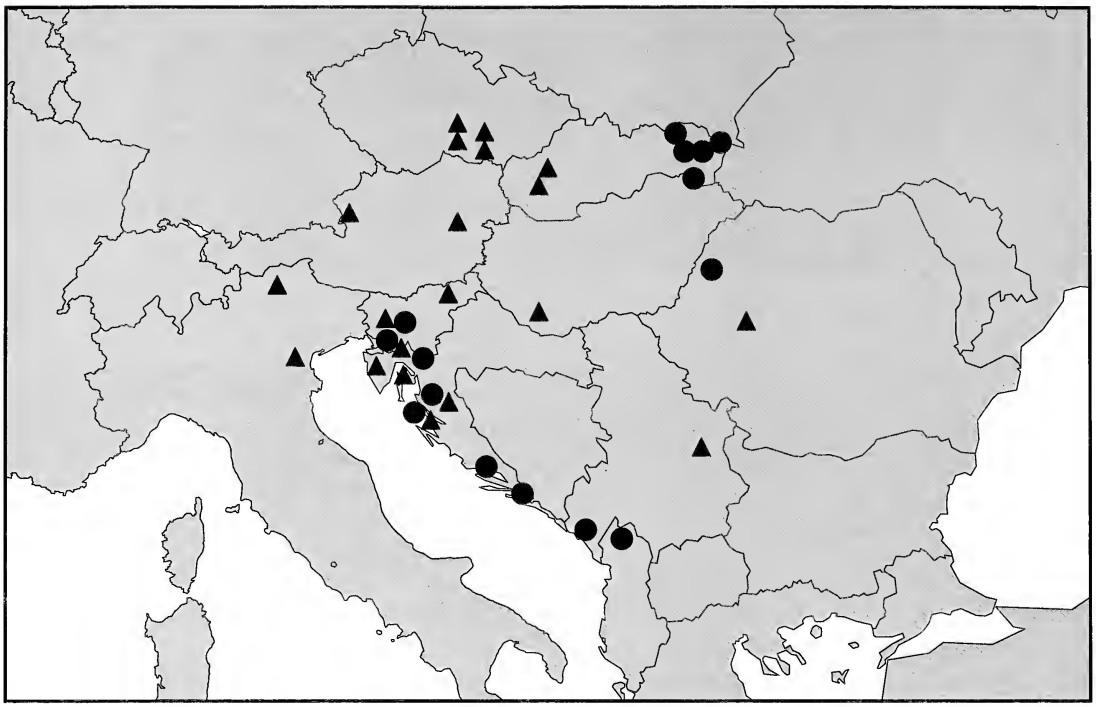


Figure 26.—Distribution of *Dysdera ninnii* (▲) and *Dysdera dubrovninnii* (●) in central Europe.

ITALY: 1 ♂, 1 ♀, Gorizia, Monfalcone [45°48′N, 13°31′E], 14 April 1991, F. Gasparo (MR); 1 ♂, 1 ♀, Trieste, Muggia, S. Floriano [45°36′N, 13°46′E], 19 April–15 May 2000, G. Colombetta (MR). ROMANIA: 1 ♀, Banat area, Carasova, Anina, Sopotu Nou [44°48′N, 21°51′E], 5–10 August 1998, V. Lemberk (MR). SLOVAKIA: 1 ♀, unspecified location, E. Žitňanská (JS). SLOVENIA: 1 ♀, Bepše pri Logatcu [45°55′N, 14°13′E], September 1934 (NMPC); 1 ♀, Kamniška Bistrica [46°20′N, 14°35′E], 8–15 August 1921, J. Hadži (NMPC); 1 ♀, Maaswald, Soča, Kranj, Unt [46°14′N, 14°16′E] (ZMHB). YUGOSLAVIA: 1 ♀, Belgrade [44°47′N, 20°28′E] (NMPC).

Diagnosis.—*Dysdera ninnii* is very similar to several species that are restricted to the Balkan and Apennine Peninsula. For diagnosis see Deeleman-Reinhold & Deeleman (1988). From other central European species, except for *D. dubrovninnii*, it differs by smooth carapace with rounded pits.

Description.—*Carapace* (Fig. 9): carapace 3.2–3.9 mm long, smooth, with rounded pits, darkly ferruginous, gibbous. Margins indented. Lateral margins of cephalic region convergent. *Chelicerae* (Figs. 9, 24): basal segment length/carapace length = 0.37. Dorsal sides of basal segments straight, smooth, covered with piligerous pits. Groove slightly elongated (length of groove/basal segment length = 0.52), equipped with three small close teeth in basal third. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Fangs elongated (fang length/carapace length = 0.35), thorn-shaped. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally usually with only a single apical spine. *Bulbus* (Figs. 10, 11): distal division with simply incurved lateral sheet projection and with flagellum. Apex with short subapical tooth. *Vulva* (Fig. 12): spermatheca almost as wide as dorsal arch. Dorsal arch wider than long. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—The oldest name related probably to this species is *D. hombergi*. Scopoli (1763) described this species as a spider with a shiny punctate carapace and shiny yellow legs. This is in contradiction with the appearance of any species of the genus *Harpactea* Bristowe 1939 for which this name is erroneously used [see also Thaler & Knoflach (2002)]. From all dysderid species occuring in the type locality "Carniola" (an ancient province in Slovenia), the type description fits two species, *D. ninnii* and *D. dubrovninnii*. The latter species is very

rare in this region, and it is likely that Scopoli described *D. ninnii*. However, his type material is probably lost; thus a definitive resolution of its identity is not possible. Therefore, we hereby designate *Aranea hombergi* as a nomen dubium.

We consider the synonymy of *D. pavesii* with *D. ninnii* (Platnick 2007) to be doubtful. In Italy, at the type locality of *D. pavesii*, several closely related species of the *ninnii* group occur. Thorell (1873) described this species based on material provided by G. Canestrini five years after Canestrini had described *D. ninnii*. Thus, Thorell was presumably aware of the existence of *D. ninnii*.

A drawing of the bulbus in Schult (1983) and perhaps also in Simon (1914), both attributed to *D. ninnii*, probably represents an undescribed species from Corsica.

Karyotype.—The male karyotype is composed of seven pairs of autosomes and a single X chromosome (Fig. 18). The sex chromosome system is thus X0.

Habitat.—In the Czech Republic and Hungary this species occurs in xerothermic forests on slopes (e.g., plant communities *Carpinion* and *Quercion pubescenti-petraeae*), in bushes (e.g., *Berberidion*) and in the shaded parts of rocky steppes (e.g., *Festucion valesiacae*). It is also common in semi-ruderal habitats, especially in the surroundings of ruins (particularly castle ruins) overgrown by bushes. In Croatia and Slovenia it occurs in lowland *Carpinus* and planted *Pinus* forests as well as in mountain *Picea*, *Fagus sylvatica*, and *Pinus nigra* forests.

Phenology.—Mating takes place from April to June, eggs are laid in June and July. Spiderlings disperse from maternal silk retreats from August to September. The spiders mature in autumn of the following year, overwinter as adults, and mate the next spring. Thus this species has a biennial life-cycle.

Distribution.—*Dysdera ninnii* is also known from the northwestern part of the Balkan Peninsula and northeastern Italy. In Slovenia and Croatia it occurs sympatrically with *D. dubrovninnii* (syntopical localities: Bač, Bepše pri Logatcu, Paklenica, Planina, Plitvička jezera, Postojna, Šibenik). The record from southern France (Simon 1914) remains to be confirmed. The northern border of its distribution runs through the Czech Republic and Slovakia, where it occurs only in the Pannonian region (Fig. 26).

The distribution maps were published by Deeleman-Reinhold & Deeleman (1988:260, map 7; for the whole area), Drensky (1938:14, map 2; for the entire area, partly based on misidentifications), Deltshev et al. (2003:251, map 19, for Serbia), Gajdoš et al. (1999: map 200, for Slovakia, together with undistinguished *D. dubrovninnii*), and Buchar & Růžička (2002:205, for the Czech Republic). The map of *D. punctata* in Gajdoš et al. (1999: map 210) probably also refers to this species.

Dysdera dubrovninnii Deeleman-Reinhold 1988
Figs. 13–16, 19, 25, 26

Dysdera dubrovninnii Deeleman-Reinhold in Deeleman-Reinhold & Deeleman 1988:184, figs. 125–128.

Type specimens.—*Dysdera dubrovninnii:* CROATIA: holotype male, Babin kuk, Dubrovnik (42°39′N, 18°05′E), 10 April 1976, J. & F. Murphy (BMNH, not examined). Paratypes: 1 female, collected with holotype (BMNH, not examined); 1 male, 2 females, Dubrovnik, 19 & 22 April 1976, J. & F. Murphy (coll. J. & F. Murphy, Hampton, UK, not examined); 3 males, 1 female, Dalmatia, Croatia (MHNG, not examined).

Material examined.—CROATIA: 1 ♂, Korčula town [42°56′N, 16°54′E], 26 August 1997, F. Gasparo (FG); 1 ♀, Lanaka [45°53′N, 17°35′E], July 1935 (NMPC); 1 ♂, 12 ♀, Velebit, national park Paklenica, surroundings of Vaganski vrh and Ivine Vodice [44°19′N, 15°28′E], 20 June 2005, M. Řezáč (MR); 1 ♀, Šibenik, Solaris [43°42′N, 15°51′E], 16–17 June 2005, M. Řezáč (MR); 1 ♀, Plitvička jezera, Korana [44°54′N, 15°35′E], 22 June 2005, M. Řezáč (MR). ROMANIA: 1 ♂, 2 ♀, Hideselu de Jos, Bihor mountains [46°57′N, 22°03′E], May–September 2004, I. Sas (MR). SLOVAKIA: *Beskydské predhorie mountains:* 1 ♂, 4 ♀, Humenné, reserve Podskalka [48°54′N, 21°55′E], 30 July–25 August 1987, 7 July 1994, 21 May–22 June 1994, 5 September 2002, V. Thomka (VMH); 1 ♀, same location, 14 August 2003, M. Řezáč (MR); 2 ♂, Kamenica nad Cirochou [48°55′N, 21°59′E], 13 August–2 November 1998, 11 May–16 July 1999, V. Thomka (VMH); 5 ♂, 1 juvenile, Kamenica nad Cirochou, Hôrka [48°55′N, 21°59′E], 13 August 1998, 20 October 1999–2 May 2000, 2 May–6 July 2000, V. Thomka (VMH); 8 ♂, 1 ♀, Kamenica nad Cirochou, Žbír

[48°55′N, 21°59′E], 18 May–30 July 2001, 18 May–30 July 2001, 30 July–26 September 2001, 29 October 2001–3 May 2002, V. Thomka (VMH); 2 ♂, Dlhé nad Cirochou [48°57′N, 22°03′E], 10 September 1998–2 June 1999, 8 September–23 October 2000, V. Thomka (VMH); 1 ♂, 1 ♀, 2 juveniles, Ptičie, reserve Humenský Sokol [48°53′N, 21°57′E], 20 May–3 August 1993, 30 June 1994, 3 October 1994, V. Thomka (VMH); 6 ♂, 3 ♀, 1 juvenile, Brekov castle [48°53′N, 21°49′E], 28 April–3 July 1998, 5 October 1998, 3 July–5 October 1998, 24 August 1999, 2 November 1999, 4 May–30 June 1999, 5 October 1998–4 May 1999, 2 November 1999–27 April 2000, V. Thomka (VMH); 1 ♀, 1 juvenile, Kamienka, Spálené mosty [48°54′N, 22°00′E], 1 October 1996–13 June 1997, V. Thomka (VMH); 21 ♂, 8 ♀, 9 juveniles, Lackovce, pod Velikou [48°56′N, 21°56′E], 4 May–2 July 2001, 2 July–31 August 2001, 23 May–9 July 2002, 12 April–23 May 2002, 5 November 2001–12 April 2002, 23 May–9 July 2002, 4 September–17 October 2002, 12 April–23 May 2002, 9 July–4 September 2002, V. Thomka (VMH). *Bukovské vrchy mountains:* 1 juvenile, Kalná Roztoka, reserve Havešová [48°58′N, 22°19′E], 27 May–30 July 1999, V. Thomka (VMH); 1 ♀, same location, 21 September 1998, J. Svatoň (JS); 1 ♂, 1 ♀, Nová Sedlica [49°02′N, 22°31′E], 15 June 1980, V. Thomka (VMH); 1 ♂, Kolbasov, reserve Bzana [49°00′N, 22°22′E], 17 May–26 July 2000, V. Thomka (VMH); 1 ♂, 2 ♀, 1 juvenile, Ošadné, reserve Hlboké [49°09′N, 22°10′E], 3 August–15 October 1999, 1 June–3 August 1999, 26 May–3 August 2000, V. Thomka (VMH); 1 ♂, Ruské, reserve Pod Ruským [49°07′N, 22°20′E], 27 October 2000–21 May 2001, V. Thomka (VMH); 1 ♂, Zboj, reserve Riaba skala [49°01′N, 22°29′E], 12 October 1994–1 June 1995, V. Thomka (VMH). *Košická kotlina basin:* 1 ♂, 1 juvenile, Prešov, castle [48°59′N, 21°14′E], 8 July 1934, F. Miller (NMPC). *Laborecká vrchovina mountains:* 1 ♂, Stakčín, reserve Hrúnok [49°00′N, 22°13′E], 11 May–26 July 2000, V. Thomka (VMH); 4 ♂, 1 ♀, 1 juvenile, Stakčín, dolina Chotínka valley [49°00′N, 22°13′E], 15 June 1995, 21 October 1999–11 May 2000, 25 July–9 October 2000, 11 May–25 July 2000, V. Thomka (VMH); 1 ♂, Snina [48°58′N, 22°09′E], 9 May–11 August 2000, V. Thomka (VMH); 2 ♂, 1 ♀, 1 juvenile, Roškovce, reserve Jarčiská [49°14′N, 21°50′E], 4 September 2001–15 March 2002, 15 March–27 May 2002, 27 May–16 July 2002, V. Thomka (VMH); 5 ♂, 3 ♀, 1 juvenile, Starina, reserve Starina [49°03′N, 22°15′E], 30 July–3 September 1999, 25 July–9 October 2000, 19 October 1999–11 May 2000, 11 May–25 July 2000, V. Thomka (VMH). *Ondavská vrchovina mountains:* 1 ♂, Humenné, Holá hora hill [48°56′N, 21°53′E], 14 November 1996, V. Thomka (VMH); 2 juveniles, Myslina [48°56′N, 21°50′E], 10 July 1995, V. Thomka (VMH); 20 ♂, 4 ♀, 1 juvenile, Humenné [48°55′N, 21°54′E], 14 October 1996, 4 October 1999, 12 June–17 August 2000, 28 April–12 June 2000, 17 August–20 October 2000, 30 April–25 June 2001, 25 June–9 August 2001, V. Thomka (VMH); 1 ♂, same location, 18–19 July 2004, F. Šťáhlavský (MR). *Spišsko-šarišské medzihorie mountains:* 2 juveniles, Kapušany, reserve Kapušianský hradný vrch [49°02′N, 21°19′E], 6 July 1934, F. Miller (NMPC); 5 ♂, 1 ♀, 1 juvenile, same location, 23 April–20 June 1996, 20 June–30 August 1996, 1 July 1997, 30 August 1996–20 May 1997, V. Thomka (VMH). *Vihorlatské vrchy mountains:* 1 ♀, Brekov, Krivošťany [48°53′N, 21°50′E], 11 September 2002, V. Thomka (VMH); 1 juvenile, Ptičie, reserve Humenské [48°53′N, 21°57′E], 12 August–21 October 2002, V. Thomka (VMH); 2 ♀, Remetské Hámre [48°51′N, 22°11′E], 27 October, F. Miller (NMPC); 7 ♂, 6 ♀, 2 juveniles, Chlmec, reserve Chlmecká skalka [48°53′N, 21°56′E], 21 September–13 November 2001, 17 June–7 August 2002, 16 April–17 June 2002, 7 August–29 October 2002, V. Thomka (VMH); 1 ♀, 4 juveniles, Jasenov pri Humennom, castle [48°54′N, 21°53′E], 26 August 1994, 28 June 1999, V. Thomka (VMH); 2 ♂, 1 juvenile, Jasenov-Hôrka [48°54′N, 21°53′E], 30 July–27 August 1987, 2–29 June 1987, 13 May–15 June 1994, V. Thomka (VMH); 1 ♀, Vinné, Vinnianské jazero lake [48°48′N, 21°58′E], 16 August 2003, M. Řezáč (MR); 7 ♀, Vinné town [48°48′N, 21°58′E], 13 July 1967, J. Vachold (PG); 7 ♂, 4 ♀, 2 juveniles, Vinné, reserve Vinnianský hradný vrch [48°48′N, 21°58′E], 3 June–31 July 1992, 9 March–3 June 1992, 13 July–19 August 1993, 19 August 1993, 22 April 1994, 22 April–24 June 1994, 8 August–26 September 1994, V. Thomka (VMH; 1 ♀, same location, 17 August 2003, M. Řezáč (MR). *Východoslovenská pahorkatina (hilly country):* 3 ♂, 2 ♀, Klokočov pri Zemplínskej Šírave [48°49′N, 22°01′E], 12 September, F. Miller (NMPC). SLOVENIA: 1 ♂, Postojna [45°46′N,

14°12′E], 25 October 1994, S. Polak (UL); 1 ♀, Bač [45°37′N, 14°16′E], 8–24 May 1994, S. Polak (UL); 1 ♀, 1 juvenile, Planina, Unška koliševka chasm [45°50′N, 14°15′E], 2000, M. Řezáč (MR); 1 ♀, Bepše pri Logatcu [45°55′N, 14°13′E], September 1934 (NMPC).

Diagnosis.—This is the only central European species of *Dysdera* that possesses dorsoventrally flattened cheliceral fangs. It is further distinguished from *D. ninnii* by the smaller body, lighter coloration, less gibbous carapace with no indented margins, and by the shape of the bulbus (e.g., lateral sheet apophysis missing, doubly incurved lateral sheet), and endogyne (narrower spermatheca).

Description.—*Carapace* (Fig. 13): carapace 2.6–4.4 mm long, smooth, with rounded pits, ferruginous, slightly gibbous. Margins not indented. Lateral margins of cephalic part convergent. *Chelicerae* (Figs. 13, 25): basal segment length/carapace length = 0.35. Basal segments dorsally convex, smooth, covered with piligerous pits. Groove slightly elongated (length of groove/basal segment length = 0.56), with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Teeth equally distant. Fangs short (fang length/carapace length = 0.28), dorsoventrally flattened. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally usually with only a single apical spine. *Bulbus* (Figs. 14, 15): distal division with hook-shaped, twice incurved lateral sheet projection and flagellum. Subapical tooth absent. *Vulva* (Fig. 16): spermatheca narrower than dorsal arch. Dorsal arch wider than long. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—*Dysdera dubrovninnii* was based on material from the countries of the former Yugoslavia and from northern Albania. Therefore, the discovery of this species in central Europe was unexpected.

Karyotype.—The male karyotype is composed of eight pairs of autosomes and a single sex chromosome (Fig. 19). Details of the male meiotic division indicated the sex chromosome system X0.

Habitat.—In central Europe, the habitats of D. *dubrovninnii* are similar to that of *D. ninnii.* It occurs on bed-rocks rich in minerals within xerothermic natural (*Quercus* spp., *Carpinus betulus*, rarely *Fagus sylvatica*) or planted forests (e.g., *Pinus* sp.). In the Balkan Peninsula it occurs in a wide range of elevations (from planted pine forests on the seashore to mountain beech forests). In southwestern Balkan (Slovenia and Croatia), where this species co-occurs with *D. ninnii*, it prefers marginal habitats such as villages, stony debris in cold chasms, steppes, alpine grasslands and mountain *Pinus mugo* bush. In comparison with *D. hungarica* it occurs on relatively more humid and more shaded habitats as evident from syntopic occurrence in Vinnianský hradný vrch hill in Slovakia.

Phenology.—Similar to that of *D. ninnii* in central Europe.

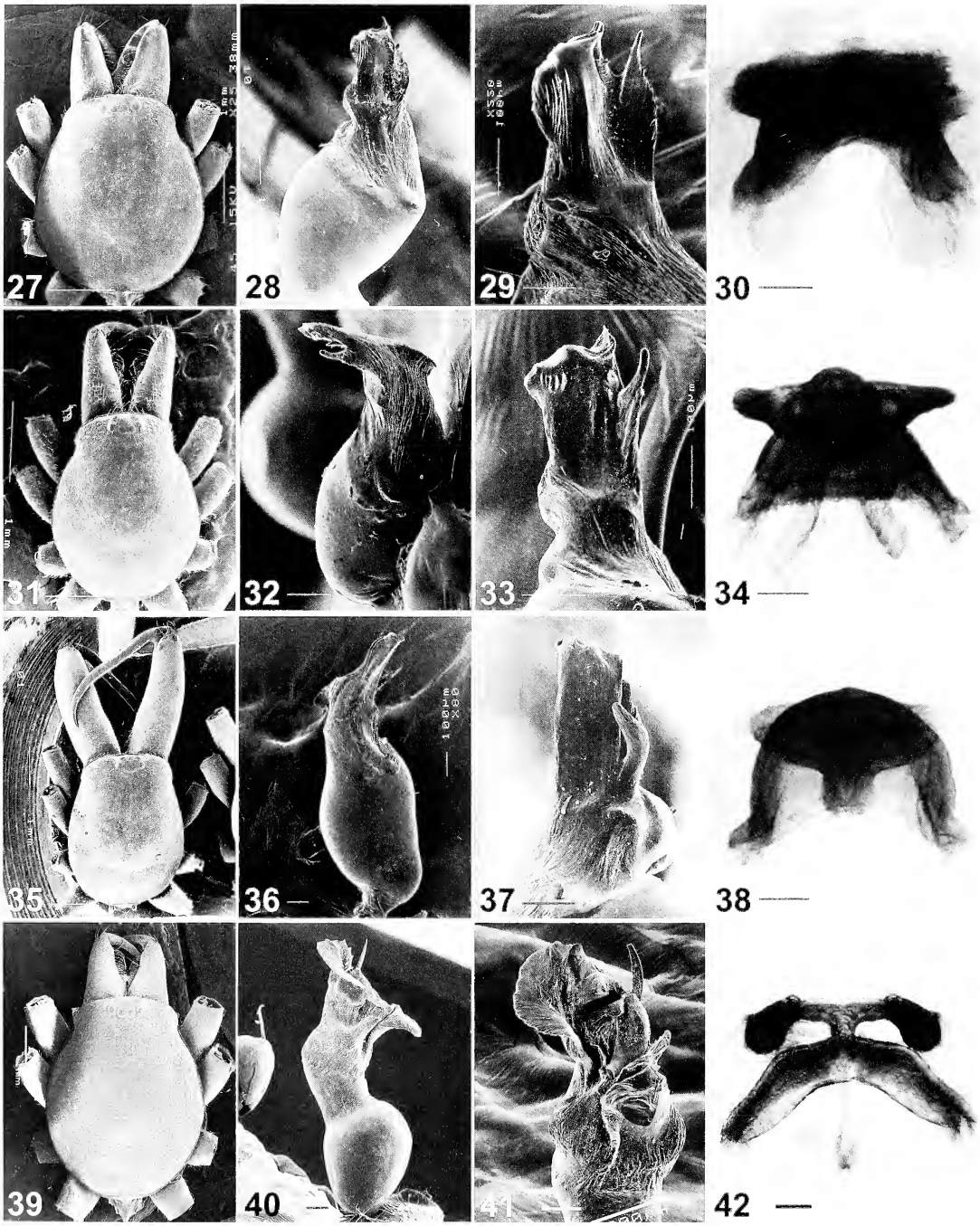
Distribution.—This species has been previously known only from the countries of the former Yugoslavia (Croatia, Slovenia, southern Montenegro) and from northern Albania (Deeleman-Reinhold & Deeleman 1988). Recently, it has been discovered in Romania and the eastern part of Slovakia, but erroneously identified as *D. ninnii* (e.g., Thomka 1997). The distribution of *D. dubrovninnii* and *D. ninnii* do not overlap in the northern part of central Europe (Fig. 26). In contrast, they occur sympatrically but rarely in the same localities in the northwest part of the Balkan Peninsula (syntopic localities in Slovenia: Bač, Bepše pri Logatcu, Postojna, Planina; Croatia: Paklenica, Plitvička jezera, Šibenik). Since *D. dubrovninnii* presumably dispersed to central Europe from northwestern Balkans, it is likely to also occur in Hungary. It probably also occurs in southeastern Poland and westernmost Ukraine, since the known localitions in eastern Slovakia are close to the Polish and Ukrainian borders. A distribution map was published by Deeleman-Reinhold & Deeleman (1988: 261, map 9). The map of *D. ninnii* in Gajdoš et al. (1999: map 200) partially refers to this species.

Dysdera longirostris species-group

Remarks.—Deeleman-Reinhold (1988) first established this species-group. Three species of the group are known from central Europe. Although they can be relatively easily distinguished, much confusion exists in the literature.

Dysdera hungarica Kulczyński 1897
Figs. 20, 27–30

Dysdera hungarica Kulczyński, in Chyzer & Kulczyński 1897:268, plate 10, fig. 42; Roewer 1928a:49, plate 7, fig. 563 (probably



Figures 27–42.—Characters of central European *Dysdera* species, *Dysdera longirostris* and *D. lata* groups. 27–30. *D. hungarica*, male from Michalovce, Slovakia; female from Prague, Czech Republic; 31–34. *D. adriatica*, male and female from Postojna, Slovenia; 35–38. *D. longirostris*, male and female from Yalta, Crimea; 39–42. *D. taurica*, male from Nidde, Turkey; female from Konya, Turkey. 27, 31, 35, 39. Male prosoma, dorsal view; 28, 32, 36, 40. Bulbus; 29, 33, 37, 41. Detail of distal division of bulbus; 30, 34, 37, 41. Anterior diverticle of vulva. Scale bars = 1 mm (prosomas), 0.1 mm (bulbi, vulvae).

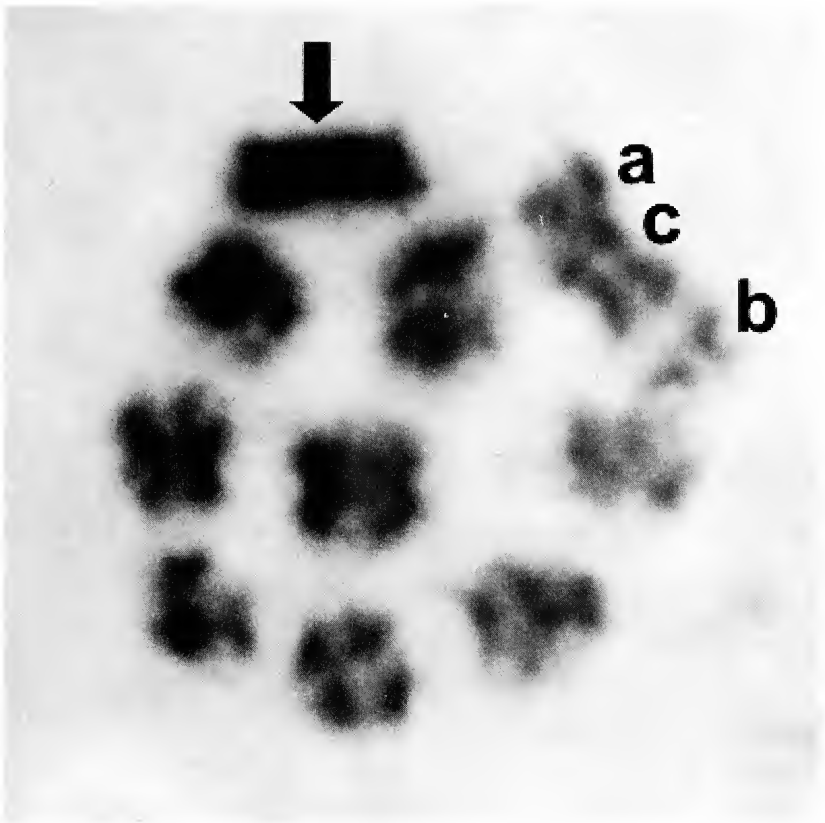


Figure 43.—*Dysdera adriatica,* male metaphase I. Note autosome trivalent (a, b – short chromosomes, c – long chromosome) and positively heteropycnotic X chromosome (arrow) on the periphery of the nucleus. Scale bar = 10 μm.

redrawn after Chyzer & Kulczyński 1897); Charitonov 1956:26, fig. 17; Loksa 1969:78, figs. 53A–C; Polenec 1985:103, fig. 8; Deeleman-Reinhold & Deeleman 1988:168, figs. 60–65; Heimer & Nentwig 1991:44, fig. 96; Dunin 1992:64, fig. 9; Řezáč & Bryja 2002:75, figs. 1–2; Thaler & Knoflach 2002:428, fig. 8.

Dysdera longirostris Doblika: Miller 1971:74, plate 5, fig. 6.

Type specimens.—*Dysdera hungarica:* syntypes: SLOVAKIA: 1 male, 7 females, Hrušov (= Körtvélyes) (48°35′N, 20°37′E), C. Chyzer (HNHM, examined). HUNGARY: unknown number of adult specimens: Satorvaralja Ujhely (48°23′N, 21°39′E), Kám (47°05′N, 16°52′E), Budapest (Kelenföld, Gellérthegy) (47°28′N, 19°02′E), Kalocsa (46°31′N, 18°59′E), Marillavölgy (47°25′N, 18°38′E) (repository unknown, not examined). ROMANIA: unknown number of adult specimens: Zalău – Meseş mountains (=Zilah – Meszeshegy) (47°10′N, 23°03′E), Cluj (=Kolozsvár) (46°46′N, 23°36′E), Gherla (=Szamosujvár) (47°01′N, 23°53′E), Alba Iulia (=Gyulafehérvár) (46°04′N, 23°34′E), Sibiu (=Nagy-Szeben) (45°47′N, 24°08′E), Haţeg (=Hátszeg) (45°36′N, 22°57′E) (repository unknown, not examined).

Material examined.—AUSTRIA: *Burgenland:* 2 ♀, Seewinkel, western Stundlacke [47°50′N, 16°40′E], 6 August–30 October 1960, J. Gruber (NMW); 3 ♀, Parndorfer Platte [47°59′N, 16°51′E], 1988–1989, K.H. Steinberger (NMW); 1 ♀, north Leithagebirge, Bruckneudorf [48°00′N, 16°46′E], 23 April 1963, J. Gruber (NMW); 1 ♀, Leithagebirge, Eisenstadt [47°50′N, 16°32′E], 8 May 1963, J. Gruber (NMW). *Nordtirol:* 5 ♀, Ahrnkopf near Innsbruck [47°12′N, 11°25′E], 1983–1984, K.H. Steinberger (NMW); 3 ♀, 1 juvenile, same location, 26 September 2005, M. Řezáč (MR). *Wachau:* 1 ♀, Dunkelsteiner Wald, Unterloiben [48°22′N, 15°31′E], 21 May 1998, J. Gruber

(NMW). *Wien:* 1♂, [48°11′N, 16°25′E], 2 July 2006, W. Nentwig (MR); 3 ♀, Wien II, Unterer Prater [48°11′N, 16°25′E], 29 March 1981, 7 June 1980, 14 December 1980, J. Gruber (NMW); 1 ♀, Wien III, Alter St. Marxer Friedhof [48°12′N, 16°21′E], 26 May–17 June 1973, J. Gruber (NMW); 4 ♀, Wien X, Laaer Wald [48°12′N, 16°21′E], 12 April 1980, 15 August 1980, J. Gruber (NMW); 1 ♀, 1 juvenile, Wien XI, Zentralfriedhof [48°12′N, 16°21′E], 2–21 June 1973, J. Gruber (NMW); 66 ♀, 3 juveniles, Wien XIX, Grinzing [48°16′N, 16°20′E], 22–26 April 1986, 26 April–18 May 1986, 1 June 1980, 12 May 1983, 17 April 1983, 3–4 April 1983, 22 May 1982, 3 September 1978, 26 July 1981, 19 June 1986, 19–23 April 1983, 13 May 1978, 10 April 1983, 29 July 1977, 27 March 1983, 20 April 1980, 15 May 1982, 27 April 1983, 19 May 1977, 2 July 1983, 2 June 1983, 30 April 1978, 11 May 1980, J. Gruber (NMW); 3 ♀, Wien XIX, Kaasgraben [48°16′N, 16°20′E], 29 September 1960, 31 May 1956, 16 May 1964, J. Gruber (NMW); 1 ♀, Bisamberg near Wien, Ortschaft [48°19′N, 16°21′E], 15 July 1989, J. Gruber (NMW). *Wiener Becken:* 1 ♀, 1 juvenile, southern Haslau [48°06′N, 16°42′E], 8 August–1 September 1960, J. Gruber (NMW); 2 ♀, southwestern Tattendorf [47°57′N, 16°17′E], 21 October 1989, J. Gruber (NMW). *Wiener Wald:* 2 ♀, Königstetten [48°18′N, 16°08′E], 24 May–22 June 1975, J. Gruber (NMW); 2 ♀, Unter-Purkersdorf [48°12′N, 16°10′E], 27 September 1980, J. Gruber (NMW). BULGARIA: 4 ♀, Kranevo near Zlatni piasaci, Varna area [43°20′N, 28°02′E], 10 August 2005, M. Řezáč (MR). CZECH REPUBLIC: *Brno:* 2 ♀, reserve Kavky [49°11′N, 16°36′E], 8 May 2004, 29 June 2005, S. Vinkler (VB); 3 ♀, reserve Obřanská stráň [49°11′N, 16°36′E], 8 May 2005, S. Vinkler (VB); 4 ♀, Kopanina [49°15′N, 16°35′E], 15 June 2005, 17 August 2005, 5 October 2005, S. Vinkler (VB). *Pálava biospheric reserve:* 1 ♀, reserve Svatý kopeček [48°47′N, 16°38′E], 14 September–22 October 2001, M. Hluchý (VB); 1 ♀, Milovický les wood [48°50′N, 16°43′E], 14 May 2003, J. Chytil (VB); 1 ♀, Mikulov, reserve Kočičí skála [48°48′N, 16°37′E], 6–11 June 1996, J. Chytil (VB); 1 ♀, Dolnodunajovický potok stream [48°51′N, 16°36′E], 21 March 2004, V. Bryja (MR); 5 ♀, Dolní Dunajovice, reserve Dolnodunajovické kopce [48°50′N, 16°33′E], 16 May–28 May 2004, 7 June–6 August 2004, 6 August–27 September 2004, S. Vinkler (VB); 2 ♀, Kinberk [48°47′N, 16°49′E], 30 September–28 November 2003, 20 March–20 May 2004, J. Chytil (VB); 3 ♀, Mikulov, reserve Slanisko u Nesytu [48°46′N, 16°41′E], 15 October 1993, J. Chytil (JS); 25 ♀, 2 juveniles, Pouzdřany, reserve Pouzdřanská step-Kolby [48°56′N, 16°37′E], 16 May–12 June 2004, 12 June–25 August 2004, 4 July–7 August 2004, 7 August–19 September 2004, 19 September–17 October 2004, 17 October–10 November 2004, 10 November 2004–4 January 2005, 12 June–12 July 2005, 12 July–6 August 2005, 30 September 2005, 28 October 2005, S. Vinkler (VB); 4 ♀, Pouzdřany, Kolby [48°57′N, 16°38′E], 30 July 1968, 25 May 1969, 20 November, 20 May, F. Miller (NMPC); 25 ♀, same location, 16 May–12 June 2004, 7 August–19 September 2004, 19 September–17 October 2004, 17 October–10 November 2004, 24 April–22 May 2005, 22 May–12 June 2005, 28 October 2005, S. Vinkler (VB). *Podyjí area:* 1 ♀, Havraníky, reserve Údolí Dyje, Šobes [48°48′N, 15°58′E], 13–17 June 1999, M. Řezáč (MR). *Prague:* 10 ♀, Ruzyně [50°05′N, 14°17′E], 22 June 1994, 30 June 1994, 15 September 1994, 23 May 1996, 10 June 1997, S. Pekár (MR). HUNGARY: 1 ♀, Velence [47°14′N, 18°39′E], 18 May 1951, L. Balogh & E. Somfai (HNHM); 1 ♀, same location, 16 June 1951, L. Vas-Borosy (HNHM); 3 ♀, 2 juveniles, Nadap, Meleghegy [47°15′N, 18°37′E], 9 June 1951, K. Zoltán (HNHM); 2 ♀, Nadap [47°15′N, 18°37′E], 24 October 1951, K. Zoltán (HNHM); 7 ♀, Pákozd, Bella völgy valley [47°13′N, 18°32′E], 9 October 1951, K. Zoltán (HNHM); 1 ♀, Alsópetény [47°53′N, 19°14′E], July 1944, I. Loksa (HNHM); 1 ♀, Györ [47°40′N, 17°38′E], July 1949, I. Andrássy (HNHM); 1 ♀, Balatonfüred, Tihany peninsula [46°55′N, 17°52′E], June 1928 (HNHM); 4 ♀, 1 juvenile, same location, 28 September 2006, M. Řezáč (MR); 1 ♀, Pécs, foot of the Misina hill [46°05′N, 18°13′E], 30 September 2006, M. Řezáč (MR); 1 ♀, Mohácsi sziget island, Kölkedi erdö forest [45°56′N, 18°42′E], 23 April 1923, E. Bokor (HNHM); 4 ♀, 2 juveniles, Szombathely, near the main railway station [47°13′N, 16°37′E], 1 October 2006, M. Řezáč (MR). ROMANIA: 2 ♀, Bucharest [44°26′N, 26°06′E], 1909, A.S. Montandon (NMPC); 1 ♂, 1 ♀, Transsylvania, 1914 (NMPC); 2 ♂, 3 ♀, Hideselu de Jos, Bihor mountains [46°57′N, 22°03′E], May–September 2004, I. Sas (MR); 2 ♀, Cluj [46°45′N,

23°57′E], 20 May 2006, W. Nentwig (MR); 1 ♂, Cluj, Suatu reserve [46°45′N, 23°57′E], 1998, I. Urák (MR); 1 ♂, mont Csik, Kászon, Salutaris [46°13′N, 26°08′E], 10–31 July 1943, Székessy (HNHM); 1 ♂, Tordai salty lake [46°33′N, 23°47′E], 10 May 1904, L. Gíró (HNHM). SLOVAKIA: *Burda mountains:* 1 juvenile, Chľaba, Kováčov [47°50′N, 18°47′E], 22 June 1960, J. Žďárek (MR); 6 ♀5 juveniles, Chľaba [47°49′N, 18°49′E], 14 August–26 October 1978, 12 September–1 November 1977, 1 June 1977–18 July 1978, 22 August–12 September 1977, V. Petřvalský (PG). *Hornonitrianska kotlina basin:* 1 ♀, Bojnice [48°46′N, 18°34′E], 11 August 1961, J. Vachold (PG). *Hronská pahorkatina (hilly country):* 2 ♀, Gbelce, reserve Parížske močiare [47°50′N, 18°30′E], 15 March–2 May 2001, 4 July–13 September 2001, P. Gajdoš (PG); 2 ♀, Paríž, reserve Gbelce [47°51′N,18°32′E], 9 May 1999, 9 May–20 May 1999, O. Majzlan (PG); 1 ♀, Mužla, Čenkov [47°47′N, 18°35′E], 20 May–27 June 1998, O. Majzlan (PG). *Košická kotlina basin:* 1 juvenile, Svinica, Bidovce [48°44′N, 21°26′E], 25 July 1995, P. Gajdoš (PG). *Kremnické vrchy mountains:* 1 ♀, Budča, reserve Boky [48°34′N, 19°04′E], 1976, V. Thomka (VMH). *Krupinská planina plain:* 1 juvenile, Krupina town [48°21′N, 19°04′E], August 1963, J. Vachold (PG); 1 ♀, Litava [48°17′N, 19°10′E], 30 September 1963, J. Vachold (PG). *Malá Fatra mountains:* 1 ♀, Terchová, Rozsutec [49°17′N, 19°00′E], F. Miller (NMPC). *Malé Karpaty mountains:* 1 juvenile, Bratislava, reserve Devínská Kobyla [48°10′N, 17°00′E], 7 April–9 May 1978, P. Gajdoš (PG); 1 ♀, Pezinok, near Chrastina [48°17′N, 17°16′E], 27 May–24 June 1994, P. Gajdoš (PG); 1 juvenile, Pezinok, Stará hora hill, Wimperegly [48°18′N, 17°16′E], 17 July–15 December 1994, P. Gajdoš (PG); 1 ♀, Stupava, Vrchná hora hill [48°17′N, 17°02′E], 23 May–19 June 1999, O. Majzlan (PG); 1 ♀, Čachtice [48°43′N, 17°47′E], 25 July 1974, J. Vachold (PG). *Ondavská vrchovina mountains:* 2 ♀, Humenné [48°56′N, 21°54′E], 22 October 1990, 20 May 1996, V. Thomka (VMH). *Podunajská rovina lowland:* 30 ♀, 10 juveniles, Bohelov [47°56′N, 17°43′E], 2 April–7 May 1992, 6 May–3 June 1992, 3 June–2 July 1992, P. Gajdoš (PG); 1 ♀, Rusovce [48°03′N, 17°08′E], P. Gajdoš (PG); 1 ♀, Bratislava-Vinohrady, Vlčie hrdlo [48°10′N, 17°08′E], 10 April 1991, O. Majzlan (PG); 2 ♀, Čilizský potok stream [47°52′N, 17°37′E], 6 May–2 June 1992, 2 June–1 July 1992, P. Gajdoš (PG); 11 ♀, Jurová [47°56′N, 17°30′E], 2 June–1 July 1992, P. Gajdoš (PG). *Považské podolie:* 1 juvenile, Trenčín [48°53′N, 18°02′E], 19 June–24 July 1998, P. Gajdoš (PG). *Slovenský kras area– Plešivecká planina plateau:* 1 ♀, Kunova Teplica, Veľký vrch hill [48°36′N, 20°22′E], 16 October 1984, J. Svatoň (JS); 2 ♀, Kružná, Veľký vrch hill II [48°37′N, 20°26′E], 23 July 1984, J. Svatoň (JS); 1 ♂, Veľká stráň [48°38′N, 20°23′E], 15 September 1983, J. Svatoň (JS); 1 ♂, Plešivec, Koniar, Hôrka [48°34′N, 20°24′E], 26 June 1984, J. Svatoň (JS). *Slovenský kras area– Silická planina plateau:* 1 ♂, Kečovo, reserve Kečovské škrapy [48°30′N, 20°28′E], 22 September 1982, J. Svatoň (JS); 1 ♂, 1 ♀, Kečovo, reserve Domické škrapy [48°28′N, 20°28′E], 25 May, F. Miller (NMPC); 1 ♀, same location, 22 September 1982, J. Svatoň (JS); 3 ♂, 2 ♀, same location, 22 August–8 October 2003, 8 October–26 November 2003, P. Gajdoš (PG); 1 ♀, Hrušov nad Turňou, reserve Hrušovská lesostep [48°35′N, 20°36′E], 23 August 1984, J. Svatoň (JS); 1 ♀, Jablonov, Hradište hill [48°36′N, 20°40′E], 16 October 1984, J. Svatoň (JS); 1 ♂, 1 ♀, Hrušov nad Turňou, Hradisko hill [48°36′N, 20°40′E], 19 August 2003, M. Řezáč (MR). *Spišsko-šarišské medzihorie mountains:* 1 ♂, Kapušany, reserve Kapušianský hradný vrch [49°02′N, 21°19′E], 31 July–9 October 1997, V. Thomka (VMH). *Tríbeč mountains:* 2 ♀, Nitra, reserve Zoborská lesostep [48°20′N, 18°06′E], 1 May 1978, 1 May 1980, P. Gajdoš (PG); 1 ♀, Velčice, reserve Velčické cery [48°24′N, 18°18′E], 22 April–22 June 1985, P. Gajdoš (PG). *Vihorlatské vrchy mountains:* 3 ♀, Vinné, reserve Vinnianský hradný vrch [48°48′N, 21°58′E], 19 August 1993, V. Thomka (VMH); 1 ♂, 1 ♀, same location, 17 August 2003, M. Řezáč (MR). *Východoslovenská pahorkatina (hilly country):* 1 ♂, 1 ♀, Velaty [48°28′N, 21°40′E], 18 August 2003, M. Řezáč (MR); 1 ♂, Vranov nad Topľou [48°53′N, 21°41′E] (MNHN); 1 ♂, 1 ♀, same location, 15 August 2003, M. Řezáč (MR). *Zemplínske vrchy mountains:* 1 ♂, 1 ♀, Veľká Tŕňa, Rozhľadňa [48°27′N, 21°41′E], 18 August 2003, M. Řezáč (MR). *Žitavská pahorkatina (hilly country):* 1 ♀, Velké Janíkovce [48°17′N, 18°08′E], 24 September 1987, V. Petřvalský (PG); 3 ♀, Nitrianské Hrnčiarovce, Malanta, way to Pohranice [48°19′N, 18°07′E], 26 June 1991, 5 May 1992, 12 November 1992, P. Gajdoš (PG). UKRAINE: *Crimea:* 1 ♀,

Cherson Taurica, Simferopol [44°57′N, 34°06′E] (NHRS); 5 ♂, 8 ♀, Kordon Bukovskogo, 35 km S of Simferopol [44°42′N, 34°07′E], 18 July 2001, N. Kovblyuk (MR); 1 ♀, Yalta, Massandra Park [44°30′N, 34°11′E], 20 May–19 June 2001, N. Kovblyuk (MR).

Diagnosis.—*Dysdera hungarica* is closely related to *D. pristiphora* Pesarini 2001 described from northern Italy and *D. hungarica atra* Mcheidze 1979 and *D. hungarica subalpina* Dunin 1992 from the Caucasus. Among central European species it is characterized by the convergent lateral anterior margins of the carapace, the bulbus is characterized by a robust tegulum and the presence of a finger-like lateral sheet apophysis, and the vulva is characterized by two parallel chitinized bands on the ventral wall of the copulatory bursa.

Description.—*Carapace* (Fig. 27): carapace 2.5–3.4 mm long, slightly wrinkled, shiny, dark brown to ferruginous, dorsoventrally flat. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 27): basal segment elongate (basal segment length/carapace length = 0.53). Inner margin straight, dorsal side convex, smooth with sparse small hairy pits. Groove elongated (length of groove/basal segment length = 0.73), equipped with three small teeth in basal half. Median cheliceral tooth > basal cheliceral tooth > distal cheliceral tooth. Median cheliceral tooth close to basal tooth. Fangs elongated (fang length/carapace length = 0.52), thorn-shaped. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with a single additional spine. *Bulbus* (Figs. 28, 29): tegulum wider than distal division. Apical part of distal division with relatively large, parallel finger-like lateral sheet apophysis. *Vulva* (Fig. 30): spermatheca straight, lateral parts almost as thick as medial part. Dorsal arch slightly wider than long. Ventral wall of copulatory bursa with paired, large, parallel chitinized bands. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—Miller (1971) erroneously attributed this species to *D. longirostris*. Among his papers, we found unpublished drawings of the same specimen in different views that enabled us to determine these specimens unambiguously as *D. hungarica*.

Karyotype.—The male karyotype is composed of eight pairs of autosomes and a single sex chromosome (Fig. 20). Analysis of male meiotic division confirmed an X0 sex chromosome system.

Habitat.—Sexual populations occur in xerothermic forests (*Quercus* spp., *Carpinus betulus*, monocultures) on bed-rocks rich in minerals. It also occurs on semirural habitats around old ruins of buildings, such as castle ruins overgrown by bushes. We noted considerable ecological plasticity of parthenogenetic clones. They occur in the same habitats as sexual populations, especially semirural woods and bushes, often with liana *Hedera helix* on the ground, and often within cities. Moreover they can occur on aforested habitats, such as wetlands with *Phragmites australis*, salt marshes, wet meadows, agroecosystems (orchards, vineyards). Low abundances are characteristic for the clones in such habitats.

Phenology.—Similar to *D. ninnii*.

Distribution.—Distribution of the nominate subspecies stretches from the Caucasus and Crimea to the Balkan Peninsula (Romania, Bulgaria) and central Europe (Hungary, Czech Republic, Slovakia, Austria). It reaches as far south as Bulgaria and Yugoslavia, and as far north as the Czech Republic and Slovakia. The subspecies *D. hungarica subalpina* is known from north Caucasus (North Osetia); *D. hungarica atra* from Georgia and Azerbaijan (Dunin 1992). Moreover, geographic parthenogenesis is present in this species (Deeleman-Reinhold 1986; Gruber 1990). In the eastern part of the distribution only sexual populations are found, while in the western part only thelytokous clones occur. The clones are characterized by isolated localities (e.g., Prague-Ruzyně). The transient zone between sexual and thelytokous forms runs through Slovakia and Hungary, specifically through Rimavská Sobota and Eger. Due to the fact that determination of members of the genus *Dysdera* is usually based on the morphology of the male copulatory organ, *D. hungarica* is largely overlooked in the western part of its distribution.

Distribution maps were published by Deeleman-Reinhold & Deeleman (1988: map 4), Deeleman-Reinhold (1986: 27, only for the central part of the distribution area, with distinguished sexual populations and parthenogenetic clones), Řezáč & Bryja (2002: fig. 3, for the Czech Republic), Buchar & Růžička (2002: 205, for the Czech Republic), Deltshev et al. (2003: map 17, for Serbia), and Gajdoš et al. (1999: map 180, for Slovakia).

Dysdera adriatica Kulczyński 1897
Figs. 21, 31–34

Dysdera hungarica var. *adriatica* Kulczyński, in Chyzer & Kulczyński 1897:270.

Dysdera adriatica: Deeleman-Reinhold & Deeleman 1988:170, figs. 66–72; Thaler & Knoflach 2002:417, figs. 1–2, 4.

Type specimens.—*Dysdera adriatica*: syntypes: CROATIA: 1 male, 1 female, 2 juveniles, Orehovica (45°19′N, 14°28′E), north Dalmatia, C. Chyzer (HNHM, examined); unknown number of adult specimens, Bakarac (45°17′N, 14°34′E), Martinšcina (=Martinscizza) (46°08′N, 16°03′E), Vrata (45°18′N, 14°43′E), Risnjak (45°25′N, 14°37′E) (repository unknown, not examined).

Material examined.—BULGARIA: 4 ♀, Bajkal near Izvor, Kiustendil area [42°26′N, 22°52′E], 8 August 2005, M. Řezáč (MR). CROATIA: 1 ♂, 12 ♀, Plitvička jezera lakes, Korana [44°54′N, 15°36′E], 22 June 2005, M. Řezáč (MR). SLOVENIA: 1 ♀, Ig. Kremenški gozd [45°56′N, 14°33′E], 7 June 1997, S. Brelih (UL); 7 ♂8 ♀, Slavnik, V. Gobovica [45°33′N, 13°58′E], 7–8 September 1996, M. Kuntner (UL); 2 ♀, Podgorje, Slavnik hill [45°31′N, 13°57′E], 26 July 1996, M. Kuntner (UL); 1 ♂, 1 ♀, Dolina Kolpe, Slavski Laz [45°29′N, 14°54′E], 29 April 2001, S. Brelih (UL); 1 ♀, Grahovo [45°46′N, 14°26′E], 6 November 1992, S. Brelih (UL). *Novo Mesto area:* 1 juvenile, Čatež near Trebnje [45°57′N, 14°57′E], 28 June 1997, M. Kuntner (UL); 1 ♀, Pleš hill near Semič [45°39′N, 15°10′E], 27 July 2001 (UL). *Lipica area:* 5 ♀, 1 juvenile, Glavica, 2 km S of Kozina [45°36′N, 13°56′E], 26 July 1996, 7 September 1996, M. Kuntner (UL). *Ljubljana area:* 1 juvenile, Ljubljana, Rašila [46°03′N, 14°30′E], July 1994, M. Jernejc (UL); 1 ♂, Rašica [45°51′N, 14°37′E], 7 April 1995, M. Kuntner (UL); 1 juvenile, Brkini, Javorje [46°13′N, 14°28′E], 25 July 1996, M. Kuntner (UL); 1 ♀, Borovnica, Pekel [45°55′N, 14°21′E], September 1996, J. Mazi (UL); 13 ♂, 5 ♀, 2 juveniles, Ljubljana, Ljubljanski vrh hill, 3 km S of Vrhnik [45°56′N, 14°17′E], 2–23 May 1996, 23 May–13 June 1996, 13 June–4 July 1996, 23 July–21 August 1996, 21 August–15 September 1996, M. Kuntner (UL). *Maribor area:* 1 juvenile, Maribor, Zgornji Duplek [46°30′N, 15°43′E], June–July 1991 (UL). *Postojna area:* 6 ♀, 1 juvenile, Planinsko polje plain [45°50′N, 14°14′E], May 1982, June 1983, 8 June 1984 (UL); 2 ♂, 3 ♀, 1 juvenile, Laze near Planinsko polje plain [45°51′N, 14°15′E], 17 July–21 August 1994, 21 September–16 October 1994, 16 October–21 November 1994, March–1 May 1995, M. Kuntner (UL; 1 ♂, June 1997, A. Gregorčič (UL); 2 ♂, 4 ♀, Razdrto [45°45′N, 14°03′E], 14 June 1957 (NMPC); 2 ♀, Planina, Unška koliševka chasm [45°50′N, 14°14′E], 2000, M. Řezáč (MR). *Kočevje area:* 1 ♂, Mahovnik near Kočevje [45°39′N, 14°50′E], 23 June 1930 (NMPC). *Ilirska Bistrica area:* 1 juvenile, Koritnice, Milanja [45°37′N, 14°16′E], 23 May 2003, S. Polak (UL); 10 ♂, 1 ♀, Koritnice, Cerje [45°37′N, 14°16′E], 1 ♂, 14 May 1994, 28 June 1994, S. Polak (UL); 4 ♂, 4 ♀, 1 juvenile, Koritnice [45°37′N, 14°16′E], 7 May 1995, 14 June 1995, 12 July 1995, 26 July 1995, 14 August 1995, S. Polak (UL); 1 ♂, Bač, Tuščak [45°38′N, 14°16′E], 4 April 1994, S. Polak (UL). *Krško area:* 1 ♀, 2 juveniles, Kozje [46°04′N, 15°33′E], 31 July, 1 August, 12 August 1999, G. Bergthaler (UL); 1 ♂, same location, 13 August 1999, M. Šuštar (UL); 1 juvenile, Krško, Pečice [46°01′N, 15°34′E], 15 May 1992, S. Brelih (UL). *Celje area:* 1 ♀, 1 juvenile, Logaška planota, near Laška Kukava, Senca [46°09′N, 15°14′E], 1–14 May 1995, 27 July–13 August 1995, M. Kuntner (UL). *Nova Gorica area:* 1 ♂, 1 ♀, Nova Gorica, Panovec [45°56′N, 13°39′E], 16 March 2001, S. Brelih (UL). *Portorož area*: 2 juveniles, Koštabona, Supot [45°29′N, 13°43′E], 24 May 1992, S. Brelih (UL). *Julijske Alpe mountains:* 1 juvenile, Zatolmin, Tolminska korita [46°11′N, 13°43′E], 10 June 1997, S. Brelih (UL); 1 ♀, Kranjska Gora, Vršič [46°28′N, 13°46′E], June 1981 (UL); 1 ♂, 2 juveniles, Čepovan– Most na Soči [46°09′N, 13°43′E], 10 June 1997, S. Brelih (UL); 1 ♂, Jesenice [46°26′N, 14°02′E], 20 September (ZMHB). *Kranj area:* 1 ♀, Kranj, Šmarjetna gora hill [46°14′N, 14°21′E], 30 June–8 July 1991, K. Prosenc (UL); 1 ♀, Udin Boršt, Spodnje Duplje, near Arnševa jama cave [46°17′N, 14°17′E], 1 August 1995, J. Kristanc (UL). YUGOSLAVIA: 1 juvenile, Vojvodina, Ruma [45°00′N, 19°49′E], 1 August 1976 (UL).

Diagnosis.—This species is very similar to *D. hungarica*, from which it differs by the smaller body, less smooth and more hairy carapace and dorsal side of basal cheliceral segment; males differ by the smaller and more protruding finger-like lateral sheet apophysis; females differ by the dorsal arch being remarkably wider than long and by the paired chitinized bands on the ventral wall of the copulatory bursa being narrow and anteriorly convergent.

Description.—*Carapace* (Fig. 31): carapace 2.3–3.4 mm long, slightly wrinkled, ferruginous, dorsoventrally flat. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 31): basal segment elongated (basal segment length/carapace length = 0.58). Inner margin of basal segment straight, dorsal side convex, with relatively dense small hairy pits. Groove elongated (length of groove/basal segment length = 0.72), with three small teeth in basal half. Median cheliceral tooth > distal cheliceral tooth > basal cheliceral tooth. Median cheliceral tooth close to basal cheliceral tooth. Fangs elongated (fang length/carapace length = 0.50), thorn-shaped. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–3 additional spines. *Bulbus* (Figs. 32, 33): tegulum wider than distal division. Apical part of distal division with protruding finger-like lateral sheet apophysis. *Vulva* (Fig. 34): Medial part of spermatheca thicker than lateral parts. Dorsal arch wider than long. Ventral wall of copulatory bursa with paired, narrow, anteriorly convergent chitinized bands. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Karyotype.—The karyotype of the sole male examined consists of 20 chromosomes (Fig. 21). Analysis of male meiotic division revealed a sex chromosome system of X0. Moreover, one large and two small autosomes form a trivalent during meiosis (Fig. 43).

Habitat.—*Dysdera adriatica* occurs in various xerothermic forests and shrubland, mainly with dominant *Carpinus betulus, Fagus sylvatica, Quercus cerris* or *Pinus nigra.*

Phenology.—Similar to that of *D. ninnii.*

Distribution.—This species occurs in the northwestern regions of the Balkan Peninsula (together with *D. ninnii* it is the most common species in Slovenia and north-western Croatia) and in the Austrian southern Alps. Since *D. adriatica* occurs in westernmost Slovenia and southernmost Austria, it is expected to also occur in northeastern Italy. Distribution maps have been published by Deeleman-Reinhold & Deeleman (1988: map 5), and Deltshev et al. (2003: map 14, only for Serbia).

Dysdera longirostris Doblika 1853
Figs. 22, 35–38

Dysdera longirostris Doblika 1853:122; Chyzer & Kulczyński 1897:218, plate 10, fig. 43; Charitonov 1956:25, fig. 11; Oltean 1962:578, fig. 2; Loksa 1969:77, figs. 53D–E, 54C; Deeleman-Reinhold & Deeleman 1988:167, figs. 51–56; Heimer & Nentwig 1991:46, fig. 97; Thaler & Knoflach 2002:418, figs. 3, 5.

Dysdera longitarsis [sic]: Herman 1879:206–207.

Type specimens.—*Dysdera longirostris:* syntypes: UKRAINE: unknown number of males and females, Crimea (perhaps NMW, not examined).

Material examined.—BULGARIA: 2 juveniles, Rilski manastir monastery [42°07′N, 23°20′E], 4 August 2005, M. Řezáč (MR); 2 ♀, Kranevo near Zlatni piasaci, Varna area [43°20′N, 28°03′E], 10 August 2005, M. Řezáč (MR); 1 ♀, Albena, Varna area [43°14′N, 28°01′E], 9 August 2005, M. Řezáč (MR); 1 ♂, Vračanski Balkan, Vratsa, Čelopeč [43°09′N, 23°27′E], 8 June 1957 (NMPC). GREECE: 1 ♂, 1 ♀, Leptokaria [40°03′N, 22°33′E], 4 June–13 June 1996, J. Dolanský (MR). HUNGARY: 1 ♀, Buda, Viranyi utca [47°30′N, 19°01′E], G. Kolosváry (HNHM); 1 ♀, Misina hill above Pécs [46°07′N, 18°12′E], 11 July 1951, Somfai (HNHM); 1 ♂, 1 ♀, same location, 30 September 2006, M. Řezáč (MR); 1 juvenile, Kölked near Mohács [45°56′N, 18°42′E], 29 September 2006, M. Řezáč (MR). MACEDONIA: 1 ♀, Šar planina [41°48′N, 20°41′E], 12 June 1974, Hladík (NMPC). TURKEY: 1 ♂, Bolu province, Düzce, Üç Köprü [40°47′N, 31°14′E], 2 May 2004, M. Horsák (MR). UKRAINE: *Crimea:* 1 ♂, 2 ♀, Cherson Taurica [44°42′N, 34°01′E] (NHRS); 3 ♂, 1 ♀, Yalta area, 1 km N of Nikitskaja School [44°29′N, 34°09′E], 3–11 June 2000, N. Kovblyuk (MR); 2 ♂, Simferopol district, 3 km NW of Skvortsovo [45°04′N, 33°48′E], 30 June–10 July 2002, N. Kovblyuk (MR). YUGOSLAVIA: 1 ♂, Belgrade [44°47′N, 20°28′E] (NMPC).

Diagnosis.—*Dysdera longirostris* is very similar to *D. hattusas* Deeleman-Reinhold 1988, a species endemic to northern Turkey. Among central European species it is characterized by the extremely elongated chelicerae. From *D. hungarica* and *D. adriatica*, the males can be further distinguished by the slender tegulum, and the medially curved finger-like lateral sheet apophysis; the females by the high, distally situated spermatheca, and by the distinct arcuate dorsal arch with the posterior extremities remarkably curved laterally.

Description.—*Carapace* (Fig. 35): carapace 3.0–3.8 mm long, wrinkled, shiny, dark brown

to ferruginous, remarkably dorsoventrally flat. Lateral margins of cephalic part convergent. *Chelicerae* (Fig. 35): basal segment very elongated (basal segment length/carapace length = 0.67). Inner margin straight, dorsal side convex, slightly wrinkled, shiny, with sparse, small hairy pits. Groove very elongated (length of groove/basal segment length = 0.87), with three small teeth in basal quarter. Median cheliceral tooth > distal cheliceral tooth > basal cheliceral tooth. Teeth equally distant. Fangs very elongated (fang length/carapace length = 0.77), thorn-shaped. *Abdomen:* in males, book lung opercula and margins of spiracles heavily sclerotized. *Legs:* femora spineless. Tibiae III–IV dorsally spineless, ventrally with a pair of apical spines and usually with 1–2 additional spines. *Bulbus* (Figs. 36, 37): tegulum slightly wider than distal division. Apical part of distal division with relatively long, medially curved finger-like lateral sheet apophysis. *Vulva* (Fig. 38): spermatheca high, in respect to dorsal arch distally situated. Dorsal arch distinctly arcuate, with posterior extremities curved laterally. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Karyotype.—The male karyotype is composed of 40 chromosomes (Fig. 22). The sex chromosome system is uncertain.

Habitat.—*Dysdera longirostris* occurs in various xerothermic forests and shrublands, often semirural ones, mainly with dominant *Carpinus betulus, Fagus sylvatica, Quercus* sp., or *Pinus* sp.

Phenology.—Similar to that of *D. ninnii.*

Distribution.—This species occurs in the Balkan Peninsula, northwestern Turkey, and Crimea. The northern border of its distribution runs through north Hungary and Romania. All records from Slovakia (Gajdoš et al. 1999: map 190) are erroneous. However, its occurence in the warmest parts of southern Slovakia, especially in the surroundings of Slovenské Nové Mesto, is possible. Distribution maps have been published by Deeleman-Reinhold & Deeleman (1988: 258, map 2), and Deltshev et al. (2003: 250, map 18, for Serbia).

Dysdera lata species-group

Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). In central Europe, the *lata* group is represented by a single species, *D. taurica.*

Dysdera taurica Charitonov 1956
Figs. 23, 39–42

Dysdera taurica Charitonov 1956:36, fig. 10; Tyschenko 1971:71, fig. 103; Deeleman-Reinhold & Deeleman 1988:208, figs. 208, 215; Heimer & Nentwig 1991:44, fig. 93.

Dysdera westringi Pickard-Cambridge: Herman 1879:205–206; Chyzer & Kulczyński 1897: 267, plate 10, fig. 39; Loksa 1969:75, figs. 52A–B; Drensky 1938:92, fig. 8b (doubtful identification).

Type specimens.—*Dysdera taurica:* syntypes: UKRAINE: 1 male, 1 female, Kekeneiz (44°24′N, 33°55′E), Crimea, 1927 (repository unknown, not examined); 1 male, 1 female, Crimea, 1947, D.M. Fedotov (repository unknown, not examined).

Material examined.—BULGARIA: 3 juveniles, Kranevo near Zlatni piasaci, Varna area [43°19′N, 28°02′E], 10 August 2005, M. Řezáč (MR). HUNGARY: 2 ♂, 1 ♀, Buda, Virányi u. [47°30′N, 19°01′E], G. Kolosváry (HNHM). ROMANIA: 1 ♂, Transylvania, Zickeli (BMNH). TURKEY: 1 ♀, Konya province, Akţehir district, Ortaköy [38°27′N, 31°31′E], 13 May 2005, T. Türket (MR); 1 ♀, Niđde province, Gümüţler town [37°59′N, 34°46′E], 4 June 2002, H. Demir (MR); 1 ♂, 1 ♀, Nidde province, Alihoca [37°29′N, 34°41′E], 18 June 2002, H. Demir (MR).

Diagnosis.—*Dysdera taurica* is the only central European *Dysdera* species possessing dorsal spines on tibiae III and IV and one of two species (with *D. lantosguensis*) possessing a concave mediodorsal margin of the basal cheliceral segment. It is very similar to members of the *lata* group, especially *D. westringi* Pickard-Cambridge 1872, *D. lata* Wider 1834 and *D. spinicrus* Simon 1882, which are restricted to the Mediterranean region, mainly the Near East. From these species the males of *D. taurica* are recognized by presence of three teeth on the apical lobe (crest) of the bulbus, and the females by the shape of the dorsal arch of the anterior diverticulum.

Description.—*Carapace* (Fig. 39): carapace 3.4–5.9 mm long, strongly wrinkled/foveated, dark brown-red to ferruginous, gibbous. Lateral margins of cephalic part parallel. *Chelicerae* (Fig. 39): basal segment slightly elongated (basal segment length/carapace length = 0.40). Dorsal side and inner margin concave, smooth, covered with dense, short hairs and several long

hairs. Groove elongated (length of groove/basal segment length = 0.52), with three small teeth in basal half. Basal cheliceral tooth > median cheliceral tooth > distal cheliceral tooth. Teeth equally distant. Fangs elongated (fang length/carapace length = 0.34), thorn-shaped. *Legs:* femora I–II spineless, femora III usually with 1, femora IV are usually with 5–6 dorsal spines. Tibiae III–IV dorsally with 1 or more spines, ventrally with a pair of apical spines and usually with 2–4 additional spines. *Bulbus* (Figs. 40, 41): tegulum long, distal part contracted. Distal division apically with a lateral lobe and a spine. Lateral lobe with three ridge-like teeth. *Vulva* (Fig. 42): spermatheca thin, the extremities dilated. Dorsal arch wider than high. For detailed description see Deeleman-Reinhold & Deeleman (1988).

Remarks.—*Dysdera taurica* has, for a long time, been identified as *D. westringi* in central Europe, but Deeleman-Reinhold & Deeleman (1988) demonstrated that *D. westringi* is in fact restricted to the eastern Mediterranean region. Central European populations belong to *D. taurica*, which was originally described from Crimea. A drawing labeled *D. westringi* in Drensky (1938) is perhaps a compilation of a figure of *D. taurica* from Chyzer & Kulczyński (1897) and a figure of *D. lata* from Simon (1914).

Karyotype.—The male karyotype is composed of 11 pairs of autosomes and a single sex chromosome (Fig. 23). Study of male meiotic plates confirmed that the sex chromosome system is X0.

Habitat.—*Dysdera taurica* occurs in xerothermic *Quercus* and *Caprinus* forests and its fringes.

Phenology.—Similar to that of *D. ninnii*.

Distribution.—This species occurs in the Balkan Peninsula, Turkey, Crimea, and on islands in the Aegean Sea. The northern border of its distribution runs through Romania, north Hungary and south Slovakia, where it occurs only in the warm limestone area of Slovak Karst. A distribution map has been published by Deeleman-Reinhold & Deeleman (1988: 264, map 14). The maps of *D. westringi* in Gajdoš et al. (1999: map 220) and in Deltshev et al. (2003: 252, map 20) actually refer to this species.

Dysdera erythrina species-group

Remarks.—This species-group was first recognized by Deeleman-Reinhold (1988). Two closely related species of this group, *D. erythrina* and *D. lantosquensis*, occur in central Europe. A more detailed study on this group is presented by Řezáč et al. (unpubl. ms.). In this contribution, we provide a list of material examined and a diagnosis.

Dysdera erythrina (Walckenaer 1802)

Material examined.—CZECH REPUBLIC: *Doupovské hory mountains:* 1 juvenile, Kadaň, reserve Úhošť [50°21′N, 13°11′E], 20 August 2004, M. Řezáč (MR). *Prague:* 3 ♂, 3 ♀, reserve Lochkovský profil [49°58′N, 14°20′E], 25 May–16 June 1960, 26 May–10 June 1961, 6–19 August 1961, 2–21 September 1961, 14 October–4 November 1961, 9 April–4 May 1960, E. Žďárková (MR); 1 ♀, reserve Cikánka [49°59′N, 14°20′E], 25 April 2004, M. Řezáč (MR); 1 ♂, 1 juvenile, reserve Slavičí údolí [49°58′N, 14°20′E], 14 October 2002, J. Strejček (MR); 2 ♀, reserve Radotínské údolí [49°58′N, 14°19′E], 20 May 2004, 3 May 2005, M. Řezáč (MR); 2 ♀, reserve Prokopské údolí [50°02′N, 14°21′E], 1995, 10 June 2003, M. Řezáč (MR); 1 ♂, 4 ♀, same location, 23 October 1976, 8 September 1979, 2 October 1976, M. Antuš (MA); 1 ♀, Dalejské údolí valley [50°02′N, 14°20′E], 2003, M. Řezáč (MR); 2 ♀, reserve Šance [49°58′N, 14°24′E], 2 April 1999, 3 May 2004, M. Řezáč (MR); 1 ♀, reserve Kalvárie [50°04′N, 14°20′E], 2004, M. Řezáč (MR); 1 ♀, Karlov [50°04′N, 14°25′E], 2004, M. Řezáč (MR); 1 ♂, Žižkov, Vítkov hill [50°05′N, 14°27′E], 18 May 1976, M. Antuš (MA); 1 ♀, Klánovice [50°04′N, 14°39′E], 28 April–10 June 2001, Š. Táborská (MR); 1 ♀, reserve Opukový lom [50°07′N, 14°17′E], 21 April 1982, J. Buchar (NMPC); 2 ♂, 4 ♀, reserve Baba [50°07′N, 14°23′E], 1 November 1978, 15 May 1979, 6 May 1979, 24 October 1979, A. Kůrka (NMPC); 2 ♂, reserve Sedlecké skály [50°08′N, 14°23′E], 23 May 1986, 18 July 1986, A. Kůrka (NMPC); 1 ♀, reserve Obora Hvězda [50°04′N, 14°19′E], 2003, M. Řezáč (MR); 3 ♂, reserve Královská obora [50°06′N, 14°25′E], 4 April 2001, J. Strejček (MR); 1 ♂, Ruzyně [50°05′N, 14°17′E], 2 July 1993, Zavoralová (NMPC); 1 ♂, 1 ♀, 1 juvenile, same location, autumn 2002, M. Řezáč (MR); 2 ♂, 1 ♀, reserve Tiché údolí, Sluneční stráň [50°09′N, 14°23′E], 16 July 1980, 4 June 1981, 2 October 1981, A. Kůrka (NMPC); 1 ♀, reserve Tiché údolí, Holý vrch hill [50°09′N, 14°22′E], 20 September 1980, A. Kůrka (NMPC); 1 juvenile, reserve

Tiché údolí, Roztocký háj [50°08′N, 14°23′E], 30 August 2003, M. Řezáč (MR). *Český kras area:* 1 ♂, Choteč, Škrábek hill [49°58′N, 14°16′E], 6 May 1959, J. Buchar (NMPC); 1 ♀, Srbsko, reserve Koda [49°55′N, 14°07′E], 6 May 1959, J. Buchar (NMPC); 1 juvenile, same location, 3 September 2003, M. Řezáč (MR); 1 ♀, 1 juvenile, Suchomasty, reserve Lom na Kobyle [49°54′N, 14°02′E], 16 June 1995, A. Kůrka (NMPC); 1 ♀, Svatý Jan pod Skalou, reserve Karlštejn [49°57′N, 14°08′E], 2003, M. Řezáč (MR); 1 ♀, Mořina, Velká Amerika quarry [49°57′N, 14°14′E], 2003, M. Řezáč (MR); 2 juveniles, Koněprusy, Čertovy schody quarry [49°55′N, 14°03′E], 8 September 1994, A. Kůrka (NMPC); 1 ♀, Koněprusy, reserve Kotýz [49°55′N, 14°03′E], 15 April 2000, M. Řezáč (MR); 1 ♂, 1 ♀, Beroun, Merhantova skála rock [49°58′N, 14°04′E], 17 June 2004, P. Špryňar (MR); 1 ♂, Suchomasty, reserve Na Voskopě [49°54′N, 14°02′E], 2 June 1999, A. Kůrka (NMPC); 1 ♂, same location, 3 August 2000, V. Pfleger (NMPC); 1 ♀, 1 juvenile, Suchomasty, Újezdce hill [49°54′N, 14°02′E], 30 July 2001, M. Řezáč (MR); 2 ♂, same location, 23 September 2001, J. Strejček (MR); 1 ♀, Karlštejn [49°56′N, 14°10′E], 6 November 1998, M. Řezáč (MR); 2 ♂, 1 ♀, 1 juvenile, Srbsko, reserve Karlštejn, Komárkova lesostep [49°56′N, 14°09′E], 3 May–30 June 1965, J. Buchar (NMPC); 1 ♂, 1 ♀, same location, 12 May 2000, 9 June 2001, M. Řezáč (MR); 4 ♀, same location, 1 August 2000, 3 October 2001, 28 October 2001, L. Kubcová (LK). *České středohoří mountains:* 1 ♂, Ústí nad Labem, Koštov [50°38′N, 13°59′E], 27 September–23 October 1995, J. Hajer (VR); 1 ♂, Ústí nad Labem, Opárenské údolí valley [50°37′N, 14°05′E], 18 June 1978, M. Antuš (MA); 1 ♂, Ústí nad Labem, Klíše, Střížovický vrch hill [50°39′N, 10°00′E], 18 April–8 May 2002, V. Hula (VH); 1 ♂, Měrunice [50°29′N, 13°48′E], 19 May 1977, A. Kůrka (NMPC); Chraberce, reserve Oblík [50°25′N, 13°49′E], 4 August 1999, M. Řezáč (MR). *Rakovnicko area:* 2 ♀, 2 juveniles, Rakovník [50°06′N, 13°43′E], 1941, F. Miller (NMPC); 1 ♀, Křivoklát [50°02′N, 13°51′E], 1941, F. Miller (NMPC); 1 ♀, Lišany [50°08′N, 13°43′E], 1941, F. Miller (NMPC). *Střední Povltaví area:* 1 ♀, Nalžovické Podhájí, reserve Drbákov-Albertovy skály [49°44′N, 14°22′E], 28 June 1991, V. Růžička (VR); 1 ♂, 2 ♀, 1 juvenile, Rabyně, Vltava valley [49°49′N, 14°25′E], 6 October 1996, 29 July 1999, M. Řezáč (MR). GERMANY: 1 ♂, 2 ♀, Hamburg [53°36′N, 10°02′E] (ZMHB); 1 ♀, 1 juvenile, Muggendorf am Nordhange [49°48′N, 11°15′E], 2 August 1908, F. Dahl (ZMHB); 1 ♂, 1 ♀, Pommelsbrunn near Nürnberg, [49°30′N, 11°30′E], 16 April 1905, F. Dahl (ZMHB); 1 ♀, Geroldsgrün [50°20′N, 11°35′E], 11 May 1905, F. Dahl (ZMHB); 2 ♂, 3 juveniles, Münster, Rothenfels an der Nahe [51°57′N, 7°38′E], 25 October 1916, F. Dahl (ZMHB); 1 ♀, 1 juvenile, Staffelstein [50°05′N, 10°58′E], 7 October 1920, F. Dahl (ZMHB); 1 ♀, Schlangenbad, Georgenborner Wand [50°05′N, 8°06′E], 27 October 1916, F. Dahl (ZMHB); 1 ♀, Doulen, Dona, 24 September, K. Verhoeff (ZMHB); 1 ♀, Wadewitzgrund, 15 June, K. Verhoeff (ZMHB); 4 ♀, Landstuhl [49°24′N, 7°34′E], C. L. Koch (BMNH); 4 ♀, Grütz [52°40′N, 12°16′E], C.L. Koch (BMNH); many ♂ ♀, Fränkischer Jura, C.L. Koch (BMNH); 3 ♂, 1 ♀, same location, L. Koch (NMW); many ♂ ♀, Würzburg [49°47′N, 9°56′E], C.L. Koch (BMNH); 1 ♀, Freiburg im Breisgau [47°59′N, 7°50′E],C.L. Koch (BMNH); 1 ♂, 1 ♀, Hartmanshof [49°28′N, 11°34′E], C.L. Koch (BMNH); 1 ♀, unspecified location (BMNH). HUNGARY: 2 ♀, unspecified location, C. Chyzer (HNHM). SLOVAKIA: 1 ♂, Belanské Tatry [49°13′N, 20°09′E], 25 July 1957, J. Žďárek (MR).

Diagnosis.—*Dysdera erythrina* is very similar to several sibling species, so far considered subspecies of *D. erythrina* [see Platnick (2007)], which are, however, restricted to northeastern Spain and southern France. It differs from the second central European member of the *erythrina* group, *D. lantosquensis*, by the convex mediodorsal margin of the basal cheliceral segment and the less wrinkled and less gibbous carapace.

Dysdera lantosquensis Simon 1882

Material examined.—AUSTRIA: *Wachau area:* 1 ♀, Spitz an der Donau, north of Roten Tor, 15 June 1996, J. Gruber (NMW); *Hainburger Berge mountains:* 1 ♀, Holfsthal [48°07′N, 16°57′E], 24 May 1959, J. Gruber (NMW). *Burgenland area:* 1 ♀, southern Leithagebirge, 14 km ENE from Wimpassing, Gaibunhal [47°56′N, 16°35′E], 11 May–29 June 1969, J. Gruber (NMW); 1 ♀, Leithagebirge, Grenzweg, Kaisereiche [47°53′N, 16°31′E], 28 June 1959, J. Gruber (NMW); 3 ♀, southern Leithagebirge, SE from Wimpassing, Lebzelter

Bg. [47°53′N, 16°28′E], 4 July 1959, J. Gruber (NMW); 1 ♀, Leithagebirge, Zeilerberg [47°55′N, 16°36′E], 17 May 1959, J. Gruber (NMW); 1 ♂, 1 ♀, Wulkaniederung, Osliper Meierhof [47°49′N, 16°36′E], 29 April 1964, J. Gruber (NMW); 1 ♀, southern Leithagebirge, Müllendorf [47°50′N, 16°27′E], 29 September 1958, J. Gruber (NMW). CZECH REPUBLIC: *Bohemia:* 2 ♂, Hradčany, reserve Báň [50°09′N, 15°16′E], 2 May–3 June 2002, J. Dolanský (JD); 1 ♀, Žehuň, reserve Žehuňský rybník [50°09′N, 15°18′E], 26 May 1961, J. Buchar (JS); 2 ♂, 1 ♀, Pardubice, Kunětická hora hill [50°04′N, 15°48′E], 4 May–18 June 1997, J. Dolanský (JD); 2 ♂, Žumberk [49°53′N, 15°52′E], 7 May 1996–10 July 1996, J. Dolanský (JD). *Moravia:* 1 ♀, Střelice near Brno, reserve Střelický les [49°08′N, 16°30′E], 28 April 1999, V. Bryja (VB); 1 ♀, Brno, Hádky [49°12′N, 16°39′E], 5 June, F. Miller (NMPC); 1 ♂, Dambořice [49°02′N, 16°56′E], 30 June 1967, F. Miller (NMPC); 1 ♂, 1 ♀, Blansko [49°20′N, 16°45′E], 15 May 1979, F. Miller (NMPC); 1 ♀, Vilémovice [49°22′N, 16°45′E], 28 September 2006, J. Vašátko (MR); 4 ♂, 2 ♀, 1 juvenile, Drslavice, reserve Terasy [49°03′N, 17°35′E], 2 June 2005, 8 August 2005, 15 September 2005, Z. Majkus (ZM); 1 ♀, Teplice nad Bečvou, near Zbrašovské aragonitové jeskyně caves [49°31′N, 17°36′E], 21 April–31 May 2004, K. Tajovský (MR); 1 ♀, Hradčovice, reserve Rovná hora [49°03′N, 17°35′E], 15 September 2005 (ZM); 1 ♀, Bruntál, reserve Ptačí hora [49°59′N, 17°27′E], 19 May 1998, Z. Majkus (JS); 2 ♂, 1 ♀, Bučovice, reserve Malhotky [49°09′N, 17°00′E], 26 June 2004, 5 September 2004, V. Hula (MR); 1 ♂, Mohelno, reserve Hadcová step [48°56′N, 16°38′E], 1983, F. Miller (NMPC); 1 ♂, same location, 10 May 1995, J. Buchar (NMPC); 1 ♀, Pouzdřany, reserve Pouzdřanská step-Kolby [48°56′N, 16°38′E], 25 October 1967, F. Miller (NMPC); 2 ♂, 2 ♀, same location, 16 May–12 June 2004, 22 May–12 June 2005, S. Vinkler (VB); 1 ♀, Horní Věstonice, reserve Děvín-Kotel-Soutěska [48°52′N, 16°38′E], 15 June 1956, F. Miller (NMPC); 1 ♂, same location, 26 October 1992–14 May 1994, V. Růžička (VR); 1 ♂, 1 ♀, same location, 2 August 2003, V. Bryja (MR). HUNGARY: 1 ♂, Miskolcz, Also-Hámor [48°05′N, 20°40′E], July 1873, O. Herman (HNHM); 2 ♂, 11 ♀, Balatonfüred, northern part of Tihany peninsula [46°55′N, 17°52′E], 28 September 2006, M. Řezáč (MR); 1 ♀, Misina hill above Pécs [46°06′N, 18°13′E], 30 September 2006, M. Řezáč (MR). SLOVAKIA: *Beskydské predhorie mountains:* 1 juvenile, Brekov [48°53′N, 21°49′E], 14 June–15 August 2000, V. Thomka (VMH). *Biele Karpaty mountains:* 3 ♂, 1 ♀, Dolná Súča, reserve Krasín [48°57′N, 18°01′E], 6 April–11 October 1989, May–11 October 1989, P. Devan (PG). *Burda mountains:* 2 ♂, 1 ♀, Chľaba, Kováčov [47°50′N, 18°46′E], 8 August 1986, 9 August 1986, P. Gajdoš (PG); 21 ♂, 16 ♀7 juveniles, Chľaba [47°49′N, 18°49′E], 14 August–26 October 1978, 6 May–20 June 1977, 12 September–1 November 1977, 1 June 1977–18 July 1978, 12 April–23 May 1977, 20 June–18 July 1977, 6 May–1 June 1977, March–12 April 1977, 12 April–6 May 1977, 12 September–2 October 1977, 22 August–12 September 1977, V. Petřvalský (PG). *Čergov mountains:* 1 ♂, 2 ♀, Hradisko [49°08′N, 21°13′E], 26 May 1936, F. Miller (NMPC). *Hornonitrianska kotlina basin:* 1 ♀, Zemianske Kostolany [48°41′N, 18°32′E], 14 May 1975 (PG). *Hronská pahorkatina (hilly country):* 1 ♀, Štúrovo [47°47′N, 18°43′E], 18 June 1964, J. Buchar (NMPC). *Kremnické vrchy mountains:* 1 ♂, 2 ♀, Budča, reserve Boky [48°34′N, 19°04′E], 1975, 1976, V. Thomka (VMH). *Malá Fatra mountains:* 1 ♂, Nezbudská Lúčka, reserve Starhrad [49°10′N, 18°51′E], F. Miller (NMPC); 1 ♀, same location, 6 May 1973, J. Svatoň (JS); 1 ♀, Strečno [49°10′N, 18°51′E], 11 May 1936, F. Miller (NMPC). *Malé Karpaty mountains:* 2 ♂, 1 juvenile, Stupava, Vrchná hora hill [48°16′N, 17°01′E], 30 April–23 May 1999, 23 May–19 June 1999, 19 June–17 July 1999, O. Majzlan (PG); 1 ♂, 2 ♀, Bratislava, reserve Devínska Kobyla [48°10′N, 17°00′E], 21 May, 21 June, F. Miller (NMPC); 1 ♂, 2 ♀, same location, 7 May 1975, 10 November 1978, O. Žitňanská (JS); 2 ♀, 2 juveniles, same location, 10 May–8 June 1979, 5 July–26 September 1979, 5 September 1980, P. Gajdoš (PG). *Myjavská pahorkatina (hilly country):* 1 ♀, Brezová pod Bradlom [48°39′N, 17°32′E], 9 June 1973, J. Vachold (PG). *Nitrianska pahorkatina (hilly country):* 2 ♂, 2 ♀, Veľký Báb, reserve Veľký Báb [48°19′N, 17°52′E], 10 May 1973, O. Žitňanská (JS). *Považské podolie:* 1 ♂, Trenčianské Bohuslavice, reserve Turecký vrch [48°47′N, 17°52′E], May–16 July 1985, P. Devan (PG). *Považský Inovec mountains:* 1 juvenile, Lúka, ruins of the castle Tematín [48°39′N, 17°52′E], 1 July 1985, P. Gajdoš

(PG); 1 ♀, Beckov, Beckovské Skalice, Dubový vŕšok hill [48°47′N, 17°53′E], May–16 July 1985, P. Devan (PG). *Revúcka vrchovina mountains:* 1 ♂, Sirk, Valašská dolina valley [48°37′N, 20°05′E], 23 September–17 October 1987, I. Mihál (JS); 1 ♂, 1 ♀, Sirk, Pod Ladislavou [48°37′N, 20°05′E], 3 June–10 July 1987, I. Mihál (JS); 1 juvenile, Sirk, Čierna dolina [48°37′N, 20°05′E], 27 August–23 September 1987, I. Mihál (JS). *Slovenský kras area– Plešivecká planina plateau:* 1 ♂, Gočaltovo, Pod Železnými vrátami [48°37′N, 20°20′E], 13 June 1983, J. Svatoň (JS); 1 ♂, Vidová, Teplá stráň [48°34′N, 20°25′E], 12 June 1983, J. Svatoň (JS); 1 ♀, Plešivec, Veľký vrch hill [48°34′N, 20°24′E], 25 June 1984, J. Svatoň (JS). *Slovenský kras area– Silická planina plateau:* 1 ♂, 1 ♀, Kečovo, Domica [48°30′N, 20°27′E], 15 May, F. Miller (NMPC); 2 ♀, 2 juveniles, same location, 22 August–8 October 2003, P. Gajdoš (PG); 1 ♀, Hrušov nad Turňou, Hradisko hill [48°35′N, 20°36′E], 19 August 2003, M. Řezáč (MR); 1 ♂, Hrušov nad Turňou, reserve Hrušovská lesostep [48°35′N, 20°36′E], 28 June 1984, J. Svatoň (JS); 1 ♂, 2 ♀, Jablonov, Hradište hill [48°36′N, 20°39′E], 16 October 1984, 24 July 1984, 16 October 1984, J. Svatoň (JS). *Spišsko-šarišské medzihorie mountains:* 1 ♀, 1 juvenile, Kapušany, reserve Kapušianský hradný vrch [49°02′N, 21°20′E], 20 June–30 August 1996, 31 July–9 October 1997, V. Thomka (VMH). *Štiavnické vrchy mountains:* 1 ♂, Počúvadlo, reserve Holík [48°21′N, 18°50′E], 13 May–17 July 1985, P. Gajdoš (PG); 1 juvenile, Tlmače, Krivín [48°16′N, 18°31′E], 4 July 1990, P. Gajdoš (PG). *Strážovské vrchy mountains:* 1 ♂, 1 ♀, Malé Krštеňany, reserve Veľký vrch [48°38′N, 18°25′E], 6 May–4 July 1984, 4 July–8 September 1984, P. Gajdoš (PG); 1 juvenile, Súľov-Hradná, reserve Súľovské skaly [49°09′N, 18°35′E], 3 July 1963, J. Vachold (PG); 1 juvenile, Bojnice, Kalvária hill [48°46′N, 18°34′E], 12 June 1991, S. Pekár (MR). *Tríbeč mountains:* 1 ♀, 2 juveniles, Nitrianska Streda, reserve Hrdovická [48°31′N, 18°10′E], 31 July–9 October 1986, 30 April–6 June 1986, 6 June–31 July 1986, P. Gajdoš (PG); 1 ♂, 1 ♀, Solčany, Úkropová [48°32′N, 18°12′E], 30 April–6 June 1986, P. Gajdoš (PG); 1 ♂, 2 ♀, Solčany, reserve Solčiansky háj [48°32′N, 18°12′E], 26 August–24 November 1987, 6 June–21 July 1987, P. Gajdoš (PG); 1 juvenile, Nitra, reserve Zoborská lesostep [48°20′N, 18°05′E], 10 May–12 June 1978, P. Gajdoš (PG). *Turčianska kotlina basin:* 3 ♂, 1 ♀, Vrútky, Chrapovský potok stream valley [49°06′N, 18°54′E], 23 July 1987, 23 July 1987, J. Svatoň (JS). *Vtáčnik mountains:* 1 ♀, Bystričany, Bystričianska dolina valley [48°39′N, 18°30′E], 3 April 1998, O. Majzlan (PG). *Zemplínske vrchy mountains:* 3 ♀, Viničky [48°23′N, 21°44′E], 12 April 1983, P. Gajdoš (PG). *Žilinská kotlina basin:* 1 ♂, 2 ♀, Žilina [49°13′N, 18°44′E], 2 May 1936, 25 May 1936, F. Miller (NMPC). *Žitavská pahorkatina (hilly country):* 9 ♂, 9 ♀, 1 juvenile, Nitrianské Hrnčiarovce, Malanta, way to Pohranice [48°19′N, 18°07′E], 5 May 1992, 11 June 1992, 11 June–15 July 1992, 25 August 1992, 25 August–29 September 1992, 12 November 1992, P. Gajdoš (PG).

Diagnosis.—*Dysdera lantosquensis* and *D. taurica* are the only central European *Dysdera* species possessing a concave mediodorsal margin of the basal cheliceral segment. In contrast to *D. taurica*, *D. lantosquensis* does not possess dorsal spines on tibiae III and IV.

DISCUSSION

Nomenclature.—The name *Aranea hombergi* Scopoli 1763 was regarded as a senior synonym of *D. ninnii* or *D. dubrovninnii*. However without access to the type material it is not possible to ascertain its exact identity. Therefore we suggest that the name *Aranea hombergi* be regarded as a nomen dubium (sensu International Commission on Zoological Nomenclature 2007). As the name *A. hombergi* was so far erroneously used for the common species of the genus *Harpactea*, the oldest synomym of this *Harpactea* species, *Harpactea latreillii* (Blackwall, 1832), should be used henceforward.

Distribution.—Nearly all species of *Dysdera* are restricted to the Palearctic region. Of the 241 species of *Dysdera* described so far, only *D. crocata* occurs outside the Palearctic region. The remaining four species (Platnick 2007) are either synonyms of *D. crocata* (the Australian *D. australiensis* and the American *D. magna*) or are misplaced in the family Dysderidae. *Dysdera solers* Walckenaer 1837, described from Colombia, possesses apically rounded gnathocoxae (Walckenaer 1837) which are never present in members of *Dysdera*. Other features mentioned by Walckenaer (1837) (e.g., the body length and orange coloration) possibly

correspond to a member of the family Caponiidae. The type material was not found in either the BMNH or MNHN. *Dysdera bicolor* Tatzanovski 1874, described from French Guyana, is only 2.5 mm long and possesses abdominal scuta (Tatzanovski 1874), which are never present in species of *Dysdera*, suggesting that it is a representative of the family Oonopidae, subfamily Gamasomorphinae. The type material was not found in either the Museum or Institute of Zoology in Warszawa or in the Museum of Natural History in Krakow. We can conclude that the genus, like all other members of the family, is originally endemic to the Palearctic region.

Patterns of distribution of *Dysdera* species in central Europe suggest limited migration abilities of these spiders. For example, *D. ninnii* is absent in the apparently climatically suitable but, by mountain range, isolated area of central Bohemia, Czech Republic. Representatives of the genus *Dysdera* are characterized by a long life and relatively low fecundity (*cf.* Cooke 1965). Thus they belong to K-selected species which do not undergo high-risk dispersal behaviors such as ballooning. Balloon dispersal has never been reported in *Dysdera* spiders, and they have never been recorded in aerial samples. For example, not a single specimen was captured among 10,000 spider specimens collected in Switzerland (Blandenier & Fürst 1998). A single ballooning dysderid recorded in Blandenier & Fürst (1998) turned out to be juvenile of *Harpactea* (Řezáč, unpublished). Nevertheless, *Dysdera* species are prone to passive accidental transport with human material due to their tendency to attach silken retreats to large objects lying on the ground. Chance dispersal by such transport is frequent among species with affinities for synanthropic habitats. The most extensive expansion of this type has been performed by *D. crocata*. Based on the distribution of its sister species, the autochthonous area of *D. crocata* is probably in the southern part of the Mediterranean, perhaps in northern Africa. Due to its adaptations to arid environments, it is able to survive a transport in dry conditions and to colonize relatively arid synanthropic habitats. Similar, yet less extensive, expansions to synanthropic habitats have also been recorded for several other species, namely *D. aculeata, D. lata, D. spinicrus, D. westringi* (Deeleman-Reinhold & Deeleman 1988), *D. kollari* (Gasparo 2004), and *D. erythrina* (a single occurrence in Slovakia). Further expansions of these species can be expected in the future.

A special preadaptation for migration is parthenogenesis within *D. hungarica*. As each adult specimen can produce eggs, thelytokous reproduction is twice as fast as bisexual reproduction where half of the population is males. Moreover, new localities can be colonized more quickly as a single individual can give rise to a new clone (Suomalainen et al. 1987). Recent expansion of parthenogenetic clones is documented in isolated locations with anthropic habitats on the western edge of the distribution of *D. hungarica* (e.g., a commercial orchard in Prague).

Habitat requirements.—In central Europe, *Dysdera* species are characteristic of warm areas, where they occur mainly in xerothermic forests on bedrocks rich in minerals. This type of biotope seems to be common for the majority of *Dysdera* species even in the Mediterranean area, i.e., the speciation center of the genus (see Deeleman-Reinhold & Deeleman 1988). In contrast to the majority of species of other central European dysderid genera, *Harpactea* and *Dasumia* Thorell 1875, *Dysdera* species usually avoid distinctly dry microhabitats in forests. Central European *Dysdera* species also occur in semi-synanthropic habitats, e.g., in the vicinity of ruins overgrown by woody plants. We suggest that an affinity for human buildings and their surrounds may be the result of rich calcium in the building materials, allowing the proliferation of woodlice, the principal prey of *Dysdera* (Cooke 1965).

In areas frequented by *D. ninnii*, the closely related species *D. dubrovninnii* is concentrated in non-forest habitats which are unusual for *Dysdera* species. Although this hypothesis is untested, we suggest that this could be a consequence of competition between these two species. A similar phenomenon was recorded from the sympatric area of *D. erythrina* and *D. crocata* in England (Cooke 1967).

Unusual ecological plasticity was observed in parthenogenetic clones of *D. hungarica*. These clones were found even in anomalous non-forest habitats such as wetlands with *Phragmites australis*, salt marshes, wet meadows, or vineyards. Thelytoky may enable the clones to survive even in suboptimal habitats, which are,

however, not suitable to harbour the high abundance necessary for sexual reproduction.

Karyotype evolution.—The genus *Dysdera* exhibits the highest variation in chromosome number of all spider genera thus far studied (Král, unpublished data). Male diploid number ranges from 9 (*D. crocata*; Díaz & Sáez 1966; this study) to 40 (*D. longirostris*, this study). Such enormous variation, as well as an absence of karyotype data from other genera of the family, renders it difficult to determine the ancestral karyotype of the genus *Dysdera*. However, due to the fact that even closely related species differ in chromosome number (*D. ninnii-D. dubrovninnii, D. hungarica-D. adriatica-D. longirostris*, this study; *D. erythrina-D. lantosquensis*) (Řezáč et al. unpubl. ms.), karyotype appears to be a useful character for the taxonomy of the genus. The high variation in chromosome numbers may be related to the holocentric structure of the chromosomes. Holocentric chromosomes exhibit kinetochore along the major part of their length. Therefore, products of chromosome fissions (fragments) or fusions (fused chromosomes) often segregate regularly to the poles during division and are then more easily tolerated than in organisms with more common monocentric chromosomes (Jacobs 2004). The structure of meiotic trivalent found in *D. adriatica* suggests that the specimen studied was heterozygous for chromosome fusion or fission. This finding supports our hypothesis about the frequent occurrence of these rearrangements in karyotype evolution in the genus *Dysdera*. Concerning sex chromosomes, we confirmed a sex chromosome system of X0 in *D. crocata* previously found by Díaz & Sáez (1966), Benavente & Wettstein (1980), Benavente (1982) and Rodríguez Gil et al. (2002). In contrast to the considerable variability in chromosome numbers, most *Dysdera* species exhibit an X0 sex chromosome system with the X chromosome being the largest chromosome. However, even number of chromosomes in male mitoses of *D. longirostris* indicates another sex chromosome system than X0. The absence of meiotic plates made impossible determination of sex chromosome system in this species.

In *D. crocata*, we also detected interpopulation polymorphism in chromosome number. Males from various populations possessed four (2n = 9), five (2n = 11) or even six (2n = 13) pairs of autosomes. A similar range of variation in chromosome numbers also has been described in South American populations of *D. crocata*. Nine chromosomes were recorded in the population called *D. magna* from Uruguay (Díaz & Sáez 1966) and 11 chromosomes in the population from Argentina (Rodríguez Gil et al. 2002). We suggest the ancestral male karyotype of *D. crocata* probably contained 13 chromosomes as this chromosome number was also found in the related species *D. gammarae* from the Iberian Peninsula (Král, unpublished). The considerable chromosome polymorphism found in *D. crocata* indicates differentiation of this species into chromosomal races or even the existence of cryptic species.

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A NEW SPECIES IN THE WOLF SPIDER GENUS *ALLOTROCHOSINA* FROM NEW SOUTH WALES, AUSTRALIA (ARANEAE, LYCOSIDAE)

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ABSTRACT. The venoniine wolf spider genus *Allotrochosina* Roewer 1960 currently includes two species, *A. schauinslandi* Simon 1899 from New Zealand (type species) and *A. karri* Vink 2001 from Western Australia. A third species of this genus, *A. walesiana* new species from New South Wales, Australia, is here described. Some differences in genital morphology of *A. walesiana* in comparison to *A. schauinslandi* and *A. karri* in combination with a misinterpretation of genitalic characters in previous treatments of the genus require a new diagnosis for *Allotrochosina*. The genus is characterized by the presence of a distinct apical process on the embolic division of the male pedipalp. *Allotrochosina walesiana* appears to be winter mature since adult spiders have only been found between June and October. Additional records of *A. karri*, which was previously only known from the type locality, Crowea in southwest Western Australia, extend the known distribution by more than 600 km to the North.

Keywords: Venoniinae, New Zealand, Western Australia, generic diagnosis

The venoniine wolf spider genus *Allotrochosina* Roewer 1960 was recently revised to include two species, *A. schauinslandi* Simon 1899 from New Zealand (type species) and *A. karri* Vink, 2001 from Western Australia (Vink 2001). *Allotrochosina* was then diagnosed by a combination of genitalic characters, such as the lack of bristles on the cymbium tip of the male pedipalp and an elongated subtegulum that is situated along the prolateral margin of the cymbium (Vink 2001). However, one of the key genitalic characters that Vink (2001) listed for *Allotrochosina*, "embolus and terminal apophysis reduced and crowded together at tip of genital bulb," was based on a misinterpretation of the morphology of the male pedipalp. The structure labeled as embolus (Vink 2001, figs. 2 & 8) is an apical process on the embolic division of the genital bulb. The actual embolus originates centrally on the embolic division and curves basally around it (Figs. 7, 8). Vink's (2001) terminal apophysis that he placed somewhere prolaterally on the embolic division does not conform to the structure that is usually referred to as "terminal apophysis" in lycosid morphology. The true terminal apophysis ("synembolus" in Zyuzin 1993; see also Framenau 2006) is usually a retrolateral, sclerotized structure on the embolic division that may protect the embolus in resting position or guide it during copulation (Figs. 4, 7, 8).

The aim of this study is to provide an updated diagnosis for the genus *Allotrochosina* incorporating new interpretations of its male genital structures and to describe a new species in this genus, *A. walesiana* sp. nov. The distribution of *A. karri*, a species that was previously only known from the type locality in southwest Western Australia, is updated.

METHODS

This study forms part of a revision of Australian wolf spiders that is based on a comprehensive examination of all wolf spider material lodged in Australian museums (ca. 20,000 records). Descriptions are based on specimens preserved in 70% ethanol. The epigynum of the paratype female was prepared for examination by submersion in lactic acid for 2 hrs. For clarity, the illustrations of male pedipalps and female epigyna omit the setae. The morphological nomenclature follows Framenau (2006) and, in case of female genitalia, Sierwald (2000). All measurements are given in millimeters (mm).

The photograph of the holotype of *A. walesiana* was taken with a digital camera (G6; Canon Inc., Japan) that was connected to the optical tube of a stereo microscope

(MZ6; Leica Microsystems GmbH, Wetzlar, Germany) with an optical adapter set (MaxView™ Plus; Scopetronix, Cape Coral, Florida, USA). Nine photographs were taken in different focal planes and combined with the software package Helicon Focus 4.0.9 (Khmelik & Kozub 2006).

Abbreviations.—*Morphology:* TL, total length; CL, CW, cephalothorax length and width; AL, AW, abdomen length and width; AE, PE anterior and posterior eyes; AME, ALE anterior median and lateral eyes; PME, PLE, posterior median and lateral eyes. *Institutions*: AM, Australian Museum (Sydney); QM, Queensland Museum (Brisbane); WAM, Western Australian Museum (Perth).

SYSTEMATICS

Family Lycosidae Sundevall 1833
Subfamily Venoniinae Lehtinen & Hippa 1979
Allotrochosina Roewer 1960

Allotrochosina Roewer 1960:927–928 (first listed as *nomen nudum* in Roewer 1955:213).

Type species.—*Lycosa maunganuiensis* Berland 1925, by monotypy [junior synonym of *Lycosa schauinslandi* Simon 1899; first synonymized by Vink (2001)].

Diagnosis.—*Male:* Macrosetae or bristles at cymbium tip absent; pedipalp tibia length subequal to length of cymbium; embolic division of male pedipalp reduced (flattened), i.e., palea absent (as in all genera of the subfamily Venoniinae sensu Lehtinen & Hippa (1979) (Framenau 2006; Yoo & Framenau 2006)); embolic division with an apical process that is directed retrolaterally (Figs. 4, 7, 8). *Female:* Genital openings extend posteriorly from epigynal area (see Vink 2001) or lateral epigynum margins extending past median septum (Fig. 5); pedipalp tibiae and tarsi subequal in length.

Remarks.—Vink (2001) attributed *Allotrochosina* to the Venoniinae based on an expanded definition of this subfamily by Dondale (1986). One of Dondale's (1986) synapomorphies of the Venoniinae was "embolus small, situated distally;" however, it has been shown recently that the embolus in species of *Venonia* Thorell 1894, the type genus of the subfamily, originates prolaterally and curves ventrally around the embolic division challenging Dondale's (1986) concept of the subfamily (e.g., Zyuzin 1993; Yoo & Framenau 2006, fig. 17D). Hence, Vink's (2001) misinterpretation of the embolus placed *Allotrochosina* in a subfamily Venoniinae *sensu* Dondale (1986) that itself was based on a misinterpretation of genitalic characters. Curiously, the placement of *Allotrochosina* in the Venoniinae *sensu* Lehtinen & Hippa 1979 was recently supported by molecular and morphological data (Murphy et al. 2006; Yoo & Framenau 2006). Similarities in particular in the embolic division of the male pedipalp support close relationships of *Allotrochosina* and the venoniine genera *Venonia* and *Anomalosa* Roewer 1960.

Included species.—*Allotrochosina schauinslandi* Simon 1899 (type species), *Allotrochosina karri* Vink 2001, *Allotrochosina walesiana* sp. nov.

Distribution.—Australia (New South Wales, Western Australia) and New Zealand.

Allotrochosina walesiana new species
(Figs. 1–6, 9)

Types.—AUSTRALIA: *New South Wales:* Holotype male, Raspberry Trap Cave, Billy's Creek, 34°06′13″S, 150°07′50″E, 22 June 1995, cave BC9-7 transition zone, S. Eberhard (AM KS53940). Paratype: 1 female, Hazelbrook, Railway Parade, 33°43′55″S, 150°27′00″E, 3 October 1996, pitfall trap, Australian Museum Business Services (AMBS), site M4 C43 (AM KS51825).

Other material examined.—AUSTRALIA: *New South Wales:* 1 ♂, 2 ♀, Blue Mountains National Park, Binnowee Drive, 33°40′15″S, 150°27′55″E, 15 August 1996 (AM KS51843–4); 1 ♂, Gordon, 33°44′S, 151°09′E, C. Horseman, 12 May 1983–9 June 1983, open *Eucalyptus* forest (AM KS12403); 1 ♀, Hazelbrook Coates Park, 33°43′45″S, 150°26′45″E, 22 August 1996 (AM KS51845); 2 ♂, 5 ♀, Hazelbrook, Railway Parade, 33°43′55″S, 150°27′00″E, 3 October 1996 (KS51829–30, KS52071–3, KS52075); 5 ♂, Hazelbrook, Winbourne Road, 33°43′20″S, 150°27′35″E, 3 October 1996 (AM KS52082–4, KS52087, KS53945); 1 ♂, 1 ♀, Woodford, Ridge Street, 33°43′50″S, 150°28′40″E, 30 September 1996 (AM KS53955–6).

Diagnosis.—Apical process of embolic division in male pedipalp of *A. walesiana* (Fig. 4) much longer than in *A. schauinslandi* or *A. karri* (Figs. 7, 8). Lateral margins of female epigy-

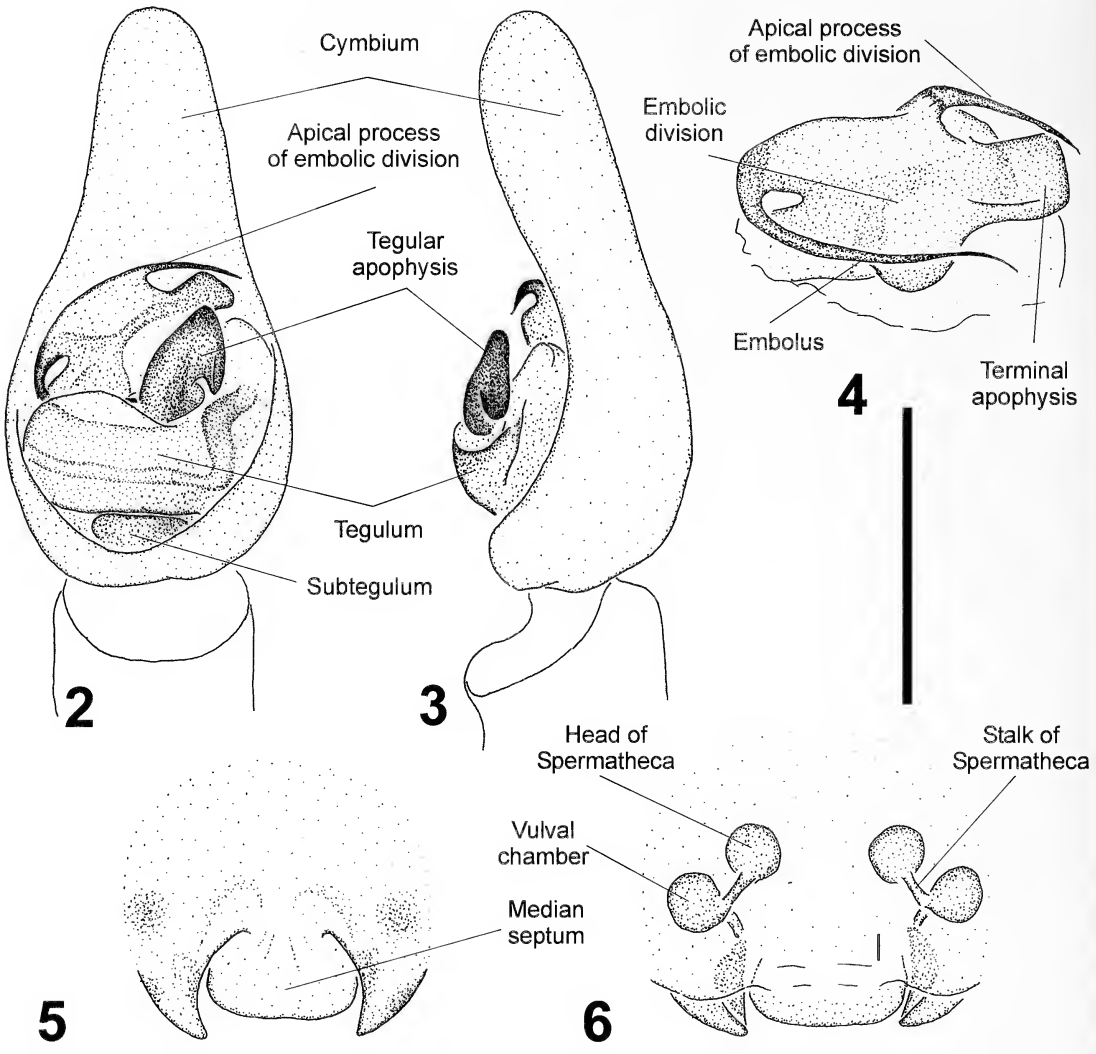
Figure 1.—Holotype male of *Alltrochosina walesiana* from Raspberry Trap Cave, New South Wales (AM KS 53940). The body length of this specimen is 8.13 mm.

num reaching past the posterior border of median septum in *A. walesiana* (median septum reaches past lateral epigynal margins in *A. schauinslandi* and *A. karri* (see Vink 2001, figs. 4, 10).

Description.—*Male (based on holotype, AM KS53940):* carapace: dorsal profile straight in lateral view; overall light brown with two faint, short longitudinal light bands in anterior half; faint traces of light submarginal bands; carapace margins darker (Fig. 1); mainly covered with dark brown setae, some white setae in longitudinal bands; black macrosetae in anterior half between fovea and eyes and around eyes; one long brown bristle between AME, six long brown bristles below AE; clypeus height about one diameter of AME. Eyes: row of AE longer than row of PME; row of AE slightly procurved. Sternum: orange-brown; covered with brown macrosetae, which are longer towards the margins. Labium: dark brown; front end truncate and white. Chelicerae: brown; brown bristles basally, otherwise long silvery setae; three retromarginal teeth, with the median largest; two promarginal teeth, with the apical larger. Pedipalp (Figs. 2–4): tegular apophysis forms an apically extended, basally directed hook; embolus long and slender with its tip pointing slightly basally, apical process of embolic division long and slender (Fig. 4). Abdomen: olive-grey with yellow lanceolate cardiac mark in anterior half, additional yellow patches and chevrons beside cardiac mark and in posterior half of abdomen (Fig. 1); covered with brown setae and macrosetae; venter yellow-brown, somewhat olive-grey mottled centrally; spinnerets brown. Legs: leg formula IV > I > II > III; brown, with very faint darker annulations; spination of leg I: femur: 3 dorsal (apical small), 1 apicoprolateral; 1 (small) retrolateral; tibia: 3 ventral pairs, 2 prolateral, 1 retrolateral (left leg only); metatarsus: 3 ventral pairs, 1 retrolateral, 1 apicoventral, 1 apicoprolateral, 1 apicoretrolateral.

Female (based on paratype, AM KS51825): carapace, eyes, sternum and labium as male. Chelicerae: coloration and setae as male; three promarginal teeth with the median largest, three (two on left chelicera) with the median (apical) largest. Epigynum (Figs. 5, 6): ventral view: lateral margins reaching posteriorly past median septum (Fig. 5); dorsal view: round spermathecal heads and thin spermathecal stalks; large, round vulval chamber (Fig. 6). Abdomen as male. Legs: leg formula IV > I > II > III; brown, apical segments somewhat darker; spination of leg I: femur: 3 dorsal (apical small), 1 apicoprolateral, 1 (small) retrolateral; tibia: 3 ventral pairs; metatarsus: 3 ventral pairs, 1 apicoventral.

Measurements: male holotype (female paratype): TL 8.13 (7.75), CL 4.38 (4.38), CW 3.25 (3.13). Eyes: AME 0.13 (0.15), ALE 0.12 (0.13), PME 0.27 (0.29), PLE 0.23 (0.21). Row of eyes: AE 0.75 (0.79), PME 0.71 (0.73), PLE 1.13 (1.19). Sternum (length/width) 2.00/1.81 (2.00/1.63). Labium (length/width) 0.77/0.63 (0.83/0.63). AL 3.75 (3.25), AW 2.25 (2.63). Legs: lengths of segments (femur + patella/tibia + metatarsus + tarsus = total length): Pedipalp 1.88 + 1.75 + — + 1.36 = 4.99; leg I 3.63 + 4.88 + 3.25 + 1.75 = 13.51; leg II 3.38 + 4.88 + 2.88 + 1.63 = 12.77; leg III 3.38 + 3.88 + 3.13 + 1.50 =



Figures 2–6.—*Allotrochosina walesiana* sp. nov. Holotype male from Raspberry Trap Cave, New South Wales (AM KS 53940): 2. Left pedipalp, ventral; 3. Left pedipalp, retrolateral. Male from Hazelbrook, Winbourne Road, New South Wales (AM KS52087); 4. Embolic division of bulb. Female paratype from Hazelbrook, Railway Parade (AM KS51825); 5. Epigynum, ventral view; 6. Epigynum, dorsal view. Scale bar: (2, 3) 0.70 mm, (4) 0.39 mm, (5, 6) 0.50 mm.

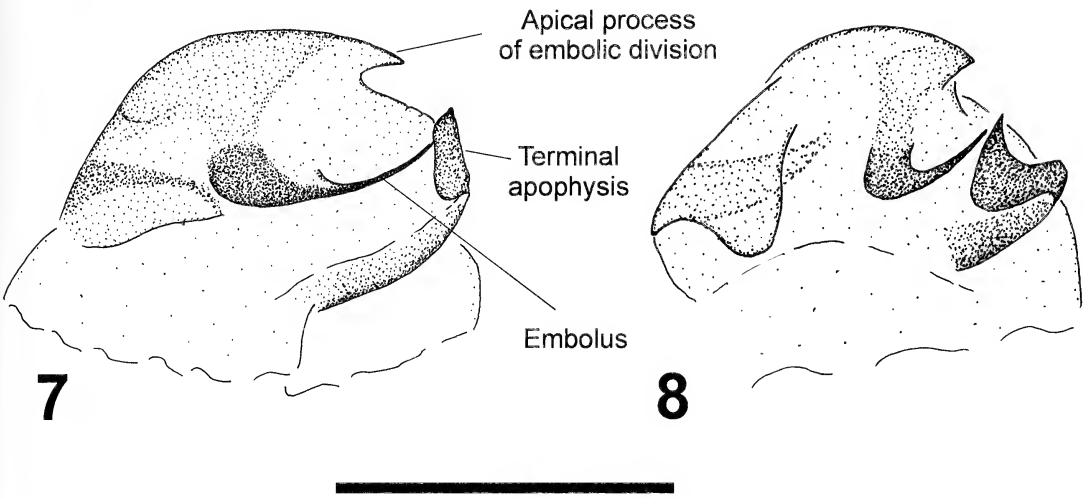
11.89; leg IV 4.13 + 5.25 + 4.75 + 2.00 = 16.13 (Pedipalp 1.75 + 1.75 + — + 1.13 = 4.63; leg I 3.50 + 4.13 + 2.75 + 1.63 = 12.01; leg II 3.13 + 3.75 + 2.38 + 1.50 = 10.76; leg III 2.88 + 3.25 + 2.63 + 1.38 = 10.14; leg IV 4.13 + 5.00 + 4.25 + 2.00 = 15.38).

Variation: ♂ (♀) (range, mean ± SD): TL 5.63–7.25, 6.73 ± 0.58; CL 3.25–3.88, 3.59 ± 0.23; CW 2.25–2.75, 2.51 ± 0.22; n = 8 (TL 6.13–10.50, 7.92 ± 1.40; CL 3.50–5.00, 4.14 ± 0.58; CW 2.50–3.50, 2.94 ± 0.35; n = 8).

Life cycle and habitat preferences.—*Allotrochosina walesiana* appears to be winter mature, as adult males and female were collected only between June and October. Not much is known about the habitat preferences of this species; the only information available is that two specimens where from a "transition zone of cave" and "open *Eucalyptus* forest."

Distribution.—*Allotrochosina walesiana* is only known from a very small range around Sydney in New South Wales (Fig. 9).

Etymology.—The specific epithet is an adjective in apposition referring to New South Wales, the Australian state where this species has been found.



Figures 7–8.—*Allotrochosina schauinslandi* Simon (1899). Male from Fox Glacier, New Zealand (WAM T40667): 7. Embolic division of bulb. *Allotrochosina karri* Vink, 2001: Male Turtle Creek, Western Australia (WAM T53823); 8. Embolic division of bulb. Scale bar: (7) 0.30 mm, (8) 0.17 mm.

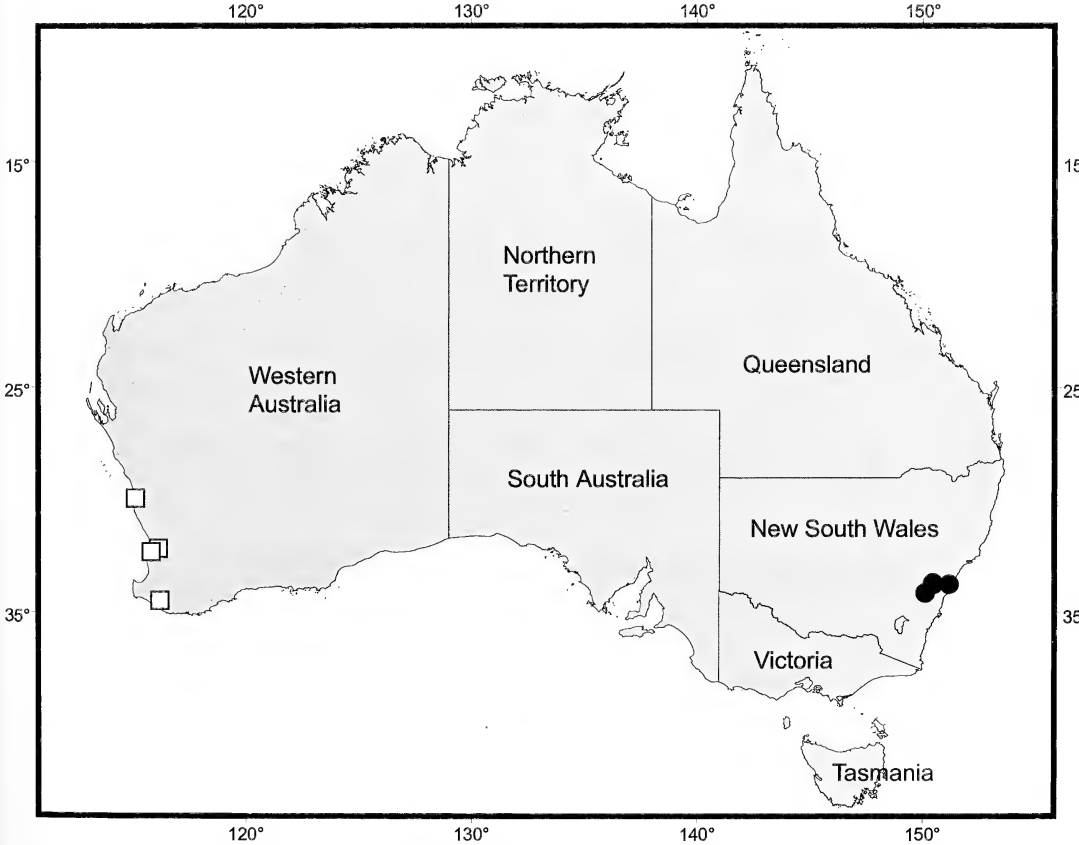


Figure 9.—Distribution records of *Allotrochosina walesiana* sp. nov. (●) and *Allotrochosina karri* Vink, 2001 (□).

Allotrochosina karri Vink 2001
(Fig. 7)

Allotrochosina karri Vink 2001:464–466, figs. 7–11.

Types.—AUSTRALIA: *Western Australia:* Holotype male, Crowea, 34°28′S, 116°10′E, week ending 31 December 1977, creek site, S J. Curry (WAM 99/114). Allotype: 1 female, Crowea, 34°28′S, 116°10′E, 20 October 1979, creek site, open (regrowth) forest, site 4A, 8/4, S.J. Curry (WAM 88/2719). Paratypes: 41 males, 13 females, Crowea, 34°28′S, 116°10′E (WAM 99/110–3, 99/115–63) (detailed collection data of all paratypes in Vink 2001). All types examined.

Other material examined.—AUSTRALIA: *Western Australia:* 1 ♀, Crowea, 34°28′S, 116°10′E, 13 December 1979, S.J. Curry, creek site, area A, 7/4 (WAM 88/2720); 1 ♀, Mt Lindesay National Park, 34°50′55″S, 117°17′56″E, 20 October 2006, M.L. Moir, J.M. Waldock, site LIND05, under sawgrass litter (WAM T77388); 1 ♀, Stockyard Cave, near Eneabba, 29°56′S, 115°06′, 27 January 1974, J. Lowry, E3, cave, near entrance (AM KS7930); 1 ♀, same locality, 26 January 1974, J. Lowry, E3, Lowry ref. no. 4/126, cave (AM KS7925); 1 ♂, 1 ♀, Stockyard Cave, Stockyard Gully, 29°56′S, 115°06′E, 17 May 1969, J. Lowry (QM W6157–8); 1 ♂, Turtle Creek, Base of Canning Dam, 32°01′16″S, 116°07′07″E, 26 August 2003, V. W. Framenau, wet litter in riparian zone (WAM T53823); 1 ♀, White Lake (= Lake Cooloongup), 32°18′S, 115°47′E, 10 February 1952, B.Y. Main (WAM T65070).

Diagnosis.—Most similar to *A. schauinslandi*, but considerably smaller (TL ca. 2.0–5.0 versus ca. 6.0–10.0); in males leg IV longest (leg I longest in *A. schauinslandi*); spermathecal stalks with 90° bend (coiled in *A. schauinslandi*) (Vink 2001).

Description.—Vink (2001) provided a detailed description of males and females of *A. karri*. Here, I illustrate the embolic division of the male pedipalp to illustrate the proper position of embolus and the apical process (Fig. 7).

Life cycle and habitat preferences.—Mature *A. karri* have been found all year round, including late autumn and winter. Recent records support previous assumptions that this species prefers damp habitats (Vink 2001), as it has mainly been collected near creeks and in gullies.

Distribution.—*Allotrochosina karri* was originally only known from the type locality, Crowea in the southwest of Western Australia. A comprehensive examination of Australian lycosid collections, in particular that of the WAM, showed that this species is more common than previously thought and its known range can be extended more than 600 km to the north (Fig. 9).

DISCUSSION

The genital morphology of *A. walesiana* differs in some aspects from *A. schauinslandi* and *A. karri*, both of which display very uniform genitalic traits. The apical process of the embolic division is much longer in *A. walesiana* and the origin of the embolus is prolateral on the embolic division (Fig. 4), whereas the embolus originates centrally in *A. schauinslandi* and *A. karri* (Figs. 7, 8). The female epigyna in the latter two species are very similar to each other with the median septum forming a posterior lip that reaches beyond the posterior margin of the epigynum. In contrast, the lateral borders of the epigynum reach beyond the median septum in *A. walesiana* and a large vulval chamber is present. However, overall similarities of somatic (e.g., coloration, eye pattern) and genitalic characters (flattened shape of embolic division, shape of tegular apophyses and internal female genitalia) leave no doubt that *A. walesiana* belongs to the genus *Allotrochosina*. The inclusion of the somewhat derived *A. walesiana* in this genus and new interpretations of male genitalic structures in comparison to Vink's (2001) review of the genus required a modification of the generic diagnosis of *Allotrochosina* as presented above. Most distinctive and unique for the genus is the apical process of the embolic division.

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A NEW HOST RECORD FOR *DASYCHERNES INQUILINUS* (ARACHNIDA, PSEUDOSCORPIONES, CHERNETIDAE), WITH AN OVERVIEW OF PSEUDOSCORPION-BEE RELATIONSHIPS

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ABSTRACT. *Dasychernes inquilinus* Chamberlin 1929, the type species of the genus, was described from specimens taken from colonies of the stingless honey bee *Melipona salti* Schwarz 1932 (Hymenoptera, Apidae). For the first time since its description, we report *D. inquilinus* from a nest of *M. compressipes* (Fabricius 1804) and, to document intraspecific variation, we also provide descriptive notes on the female pedipalp and leg. We discuss the rareness of *D. inquilinus* and summarize published information on pseudoscorpion-bee relationships. We found a total of 15 pseudoscorpion species (six genera in three families) reported from colonies of three stingless bee species and two honey bee species. The role of pseudoscorpions within bee nests is still poorly known. Like our notes on *D. inquilinus*, most records of pseudoscorpion-bee relationships are sporadic observations, sparsely reported in the literature.

Keywords: Taxonomy, Colombia, neotropical, stingless bees, honey bees

The purposes of this note are to report *Dasychernes inquilinus* Chamberlin 1929 (Arachnida, Pseudoscorpiones, Chernetidae) from a nest of the stingless honey bee *Melipona compressipes* (Fabricius 1804) (Hymenoptera, Apidae, Meliponini), and summarize published information on pseudoscorpion-bee relationships. *Dasychernes* Chamberlin 1929, a Neotropical genus of melittophilous pseudoscorpions or pseudoscorpions exclusively associated with bees, contains four species associated with colonies of the stingless bee genera *Melipona* Illiger and *Trigona* Jurine (Mahnert 1982, 1987; Harvey 1991). *Dasychernes inquilinus*, the type species of the genus, was described from specimens collected inside two colonies of *Melipona salti* Schwarz 1932 (= *M. interrupta* Latr. var. *salti*) on the Caribbean coast of Colombia (Chamberlin 1929; Salt 1929; Mahnert 1982). In addition to representing a new host association, the record of *D. inquilinus* is noteworthy because of the rareness of this species. Despite the amount of stingless bee research and beekeeping in the tropical regions of the Americas, *D. inquilinus* has not been more frequently recorded.

We found a total of 15 pseudoscorpion species (six genera in three families) reported from colonies of three stingless bee species and two honey bee species (*Apis* Linnaeus) (Table 1). The role of pseudoscorpions within bee nests is still poorly known, and like our observations on *D. inquilinus*, most records of pseudoscorpion-bee relationships are sporadic, sparsely reported in the literature. We hope to draw more attention to and encourage future studies on the ecological role of these interesting associations.

On December 2004, we found specimens of *D. inquilinus* while transferring a wild colony of *M. compressipes* to a wooden box. This bee colony was found in Cunday, Departamento of Tolima (4°00′5.5″N, 74°74′4.4″W; ~500 m elev.), Colombia, inside a cavity formed by rocks at 40 cm above the ground.

Voucher specimens of *D. inquilinus* are deposited in the Geneva Natural History Museum, Switzerland (MHNG) (1 ♀, 1 ♂

Table 1.—Melittophilous pseudoscorpions and their hosts or commensals. Bee host/commensal: 1 = the presence of *C. cancroides* inside *A. mellifera* colonies seems to be sporadic because it has also been reported from mammal and bird nests, and human constructions (Donovan & Paul 2005; Villegas-Guzman & Pérez 2006); 2 = due to morphological similarity between *Dasychernes* and *C. sellowi*, the only species of *Corosoma*, it has been suggested that the latter genus might also be associated with stingless bees (Mahnert 1982, 1987).

Species	Bee host/commensal	Location	References
CHELIFERIDAE	APIDAE: APINI		
Chelifer cancroides (Linnaeus 1758)	*Apis mellifera* Linnaeus 1758[1]	Cosmopolitan	Donovan & Paul 2005
Ellingsenius fulleri (Hewitt & Godfrey 1929)	*A. mellifera*	Spain, Cyprus, Iran, Oman, South Africa	Beier 1948; Judson 1990; Donovan & Paul 2005
E. globosus Beier 1962	*A. mellifera*	Rwanda	Beier 1948; Donovan & Paul 2005
E. hendrickxi Vachon 1954	*A. mellifera*	Zaire	Beier 1948; Donovan & Paul 2005
E. indicus Chamberlin 1932	*A. mellifera, A. cerana* Fabricius 1793	India	Beier 1948; Subbiah et al. 1957; Murthy & Venkataramanan 1985, 1986; Donovan & Paul 2005
E. sculpturatus (Lewis 1903)	*A. mellifera*	California (USA), Namibia, Zaire, Zimbabwe, South Africa	Beier 1948; Harvey 1991; Donovan & Paul 2005
E. perpustulatus Beier 1962	*A. mellifera*	Kenya	Beier 1948; Donovan & Paul 2005
E. ugandanus Beier 1935	*A. mellifera*	Uganda	Beier 1948; Donovan & Paul 2005
CHERNETIDAE			
Chernes cimicoides (Fabricius 1793)	*A. mellifera*	Austria	Beier 1948
	APIDAE: MELIPONINI		
Corosoma sellowi Karsch 1879	Meliponini[2]	Brazil	Mahnert 1982, 1987
Dasychernes inquilinus Chamberlin 1929	*Melipona salti* Schwarz 1932, *M. compressipes* (Fabricius 1804)	Colombia	Salt 1929; this work
D. panamensis Mahnert 1987	*Trigona nigerrima* Cresson 1878	Panama	Mahnert 1987
D. roubiki Mahnert 1987	*T. nigerrima*	Panama	Mahnert 1987
D. trigonae Mahnert 1987	*T. nigerrima*	Panama	Mahnert 1987
WITHIIDAE	APIDAE: APINI		
Withius simoni (Balzan 1892)	*A. mellifera*	South Africa	Beier 1948

and 1 tritonymph), the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, and in the Museo Javeriano de Historia Natural Lorenzo Uribe, Pontificia Universidad Javeriana, Bogotá, Colombia (2 ♀, 2 ♂, 2 tritonymphs, 4 deutonymphs, and 3 protonymphs).

Biological observations.—We counted at least ten individuals (males, females, and immatures) of *D. inquilinus* crawling inside the inner walls of the bee nest cavity, as well as over bee fecal masses within the nest and brood combs containing old bee pupae (Fig. 1). We also found an oviposition or molting chamber of *D. inquilinus* made inside an empty bee cell. This chamber was built up by a whitish silk membrane and had a single *D. inquilinus* adult. We did not make any effort to quantify and locate all *D. inquilinus* individuals to avoid damaging the bee colony.

Figure 1.—The melittophilous pseudoscorpion, *Dasychernes inquilinus*, on a *Melipona compressipes* brood comb from a nest found in central Colombia.

Taxonomic observations.—The two adult specimens of *D. inquilinus*, deposited in MHNG, possess the morphological and morphometric characters indicated in the original description and subsequent publications (Chamberlin 1929, 1931; Mahnert 1982). To further document intraspecific variation, the following are additional comments on the female pedipalp and leg: pedipalp indistinctly granulate, chela hand near base of movable finger with a cluster of finely dentate setae, both chelal fingers externolaterally with numerous sense spots, lateral side of fixed finger with numerous microchaetae in distal quarter; fixed finger with approximately 95 small marginal teeth, 15 externolateral accessory teeth and 7 internolateral accessory teeth, movable finger with approximately 85 marginal teeth, 13 externolateral, and 9 internolateral accessory teeth; nodus ramosus of venom duct at level of trichobothrium *t*. Setae on leg I of equal length, finely dentate and acute, setae on leg IV distinctly longer than those of leg I, the ventral setae on femur + patella longer than lateral and dorsal ones, dorsal setae of tibia distinctly longer than the ventral ones (like those in species of *Pachychernes* Beier 1932, but less numerous), tarsus without tactile seta.

Measurements (in mm): total length 5.00; cephalothorax 1.50/1.90; pedipalps: trochanter 2.0 times longer than broad (0.93/0.47), femur 2.9 times (1.48/0.50), patella 2.7 times (1.40/0.51), chela hand with pedicel 1.9 times (1.27/0.66), movable finger 1.17 times longer than hand with pedicel, length 1.49, chela with pedicel 4.0 times longer than broad, length 2.64; leg I: femur 1.55 times longer than deep (0.63/0.40), patella 1.5 times longer than femur and 2.7 times longer than deep (0.96/0.35), tibia 4.0 times (0.89/0.22), tarsus 5.0 times (0.87/0.17); leg IV: femur + patella 3.6 times longer than deep (1.70/0.48), tibia 5.7 times (1.32/0.23), tarsus 5.6 times (1.05/0.19).

Pseudoscorpion-bee relationships.—The presence of adults and immatures of *D. inquilinus* inside the nest cavity, as well as the oviposition or molting chamber within the brood comb of *M. compressipes*, suggest that *D. inquilinus* was not only occupying but also reproducing within the nest at the time it was found. These observations are similar to those of Salt (1929) on *D. inquilinus* inside *M. salti* nests.

Dispersal by phoresis is common among pseudoscorpions in the family Chernetidae (e.g., Muchmore 1971; Zeh & Zeh 1992a, 1992b; Aguiar & Bührnheim 1998). Pseudoscorpions associated with *Apis* could disperse long distances when the colony swarms, as it has been observed in *Ellingsenius indicus* Chamberlin 1932 (Murthy & Venkataramanan

1985, 1986). This might not be the case for those associated with stingless bees. Unlike *Apis*, new colonies of stingless bees depend entirely for weeks or months upon the mother colony. Thus, a new colony is usually very close to the old one, with workers bringing back and forth nesting materials and food (Michener 2000). If pseudoscorpions are present in one colony, then they are likely to be found in other nearby colonies. Likewise, host switching in melittophilous pseudoscorpions is likely to occur when bees forage for food or nesting materials on the same flower or collecting areas. For example, stingless bee colonies rapidly acquire flightless scotocryptine beetles (Coleoptera, Leiodidae) in this manner, when infested colonies are introduced to the same area (Roubik & Wheeler 1982). This suggests that melittophilous pseudoscorpions might disperse in the same way. In addition, although there is no evidence, melittophilous pseudoscorpions might also disperse using parasitic bees. For instance, *Dasychernes* could disperse during the attacks of *Lestrimelitta* Friese, a genus of cleptoparasitic stingless bees. *Lestrimelitta* is widely distributed in the Neotropical region and forage exclusively on nests of other stingless bees, including colonies of *Melipona*, *Trigona* and sometimes *Apis* (Michener 2000).

The two *Melipona* species associated with *D. inquilinus* (*M. salti* and *M. compressipes*), although widely spread in Colombia, are not commonly found (Gonzalez, pers. obs.). While we found 21 nests of *M. fuscipes* Friese, we only found one nest of *M. compressipes* despite an intensive survey in more than 400 hectares in Cunday (Mantilla, pers. obs.). Considering the phoretic means of dispersal and potential host switch, it would seem likely to find *D. inquilinus* associated with other abundant sympatric species, such as *M. fuscipes*. However, no individuals of *D. inquilinus* have been observed in any of the *M. fuscipes* colonies examined thus far.

Due to their small size and their smooth, slow movements or long periods of immobility, pseudoscorpions might be overlooked inside bee colonies by bee biologists. However, the large size of *D. inquilinus* (5–6 mm, about half as long as the bees) would make them more conspicuous than other pseudoscorpions. Surprisingly, despite the amount of stingless bee research and beekeeping in the tropical regions of the Americas, *D. inquilinus* has not been more frequently recorded. The only record that might correspond to *D. inquilinus* is that of Beier (1948), who mentioned an unidentified pseudoscorpion from a colony of *Melipona scutellaris* Latreille 1811 (= *Melipona mutata* Lepeletier 1836) in Pará, Brazil. It is likely to be *D. inquilinus* because this is the only species associated with *Melipona* colonies, but without examining the specimens, this record is still uncertain. Therefore, *D. inquilinus* seems to be specific to certain *Melipona* species and/or host switching is apparently not very common in this species. These suggestions are strengthened by the facts that no individuals of *D. inquilinus* have been observed in any of the colonies of *M. fuscipes*, a locally abundant sympatric species with *M. compressipes*, and that it has not been more frequently recorded, despite its large size and amount of stingless bee research and beekeeping in tropical America.

Like our observations on *D. inquilinus*, most records on pseudoscorpion-insect relationships are sporadic and, except for the works of Beier (1948), Muchmore (1971), and Aguiar & Bührnheim (1998), sparsely reported in the literature. We found records for a total of 15 pseudoscorpion species (six genera in three families) reported from colonies of three stingless bee species and two honey bee species (Table 1). Species of the genera *Dasychernes* and *Ellingsenius* Chamberlin 1932, and probably *Corosoma* Karsch 1879, a monotypic genus showing morphological similarities to *Dasychernes*, are apparently exclusively associated with bee colonies. There are no obvious morphological characteristics associated with a melittophilous life style. However, *Corosoma* and *Dasychernes* have abundant vestitural setae (Mahnert, pers. obs.), and we speculate that might help them in disguising themselves from the host. Other pseudoscorpions reported from bee colonies seem to be fortuitous cases. For example, the cosmopolitan *Chelifer cancroides* (Linnaeus 1758) has been collected from colonies of *Apis mellifera* Linnaeus as well as from mammal and bird nests, and even human constructions (e.g., Donovan & Paul 2005; Villegas-Guzman & Pérez 2006).

The role of pseudoscorpions within bee nests is still poorly known. The predatory habits of pseudoscorpions suggests that they might prey on aged, decrepit, or sick bees and possibly other associated arthropods inside the colony, including pests. For instance, in colonies of *Apis mellifera* and *A. cerana* Fabricius 1793, *E.*

indicus preys on *Varroa destructor* Anderson & Trueman 2000, a mite that frequently causes the death of an entire colony by feeding on the haemolymph of both adult and immature bees (Donovan & Paul 2005, 2006). Thus, some pseudoscorpion species might be beneficial for beekeepers but certainly negative effects on bee colonies cannot be ruled out. Further studies of the ecological role of pseudoscorpions within bee colonies are needed.

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HUNTING THE HUNTERS: SPATIAL AND TEMPORAL RELATIONSHIPS OF PREDATORS THAT HUNT AT THE SAME SITES

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ABSTRACT. Newly emerged crab spiderlings *Misumena vatia* (Clerck 1757) that recruit to goldenrod *Solidago* spp. inflorescences are subject to predation by small jumping spiders (Salticidae), principal among them being middle-instar *Pelegrina insignis* (Banks 1892). I censused goldenrod inflorescences to determine whether the distribution and abundance of crab spiderlings and small jumping spiders were related to one other. The censuses demonstrated a modest negative relationship in the presence of the two species to each other on the inflorescences of goldenrod clones. On inflorescences cleared of spiders and stocked with 20 dyed crab spiderlings, a strongly negative relationship occurred between numbers of recruiting jumping spiders and crab spiderlings on the first two days, but on the third and fourth days a significant positive relationship occurred. A similar pattern occurred on clones cleared of spiders and stocked with 20 spiderlings and three jumping spiders, but the shift to a positive relationship took place after a single day. This shift in behavior apparently occurred after the spiderlings found satisfactory hiding and hunting sites. Seventeen of the 39 jumping spiders captured at these sites during the two experiments had dye on their mouthparts, indicating that they had captured crab spiderlings during this time.

Keywords: Araneae, spiders, *Misumena*, Salticidae, intraguild predation

Although ecologists have traditionally portrayed trophic relationships as simple food chains with two levels of predators, primary and top predators, it is often not appreciated that the relationship between members of these two levels may reverse itself; that is, trophic levels 3 and 4 might change to levels 4 and 3, respectively (e.g., Rypstra & Samu 2005; Morse 2006). The phenology of these species is often not in close synchrony, and thus the relative sizes and relationships of any two such species may vary greatly over time. In that some predators routinely capture prey that are extremely large relative to their own size, which species is predator and which is prey in these interactions may routinely shift over their respective life cycles. Such intraguild predation (Polis 1981) can subsequently affect not only these predators, but their herbivorous prey and, indirectly, the latter's food plants as well (Polis et al. 1989; Holt & Polis 1997; Arim & Marquet 2004).

As highly aggressive predators that hunt over their entire free-living lifetimes, during which their mass may span over three orders of magnitude, spiders present a particularly striking, though not unique, life style. Both conspecifics with slightly different emergence times and species with somewhat different phenologies, the subject of this paper, may differ in size within and between themselves at any given time. Most significantly, at certain seasons members of the smaller species may exceed the size of the larger species. Since small species often have earlier reproductive periods than larger species (Foelix 1996), this relationship is not unusual (e.g., Hodge 1999; Balfour et al. 2003; Rypstra & Samu 2005). However, it may significantly impact the behavior (see Lima & Dill 1990; Lima 1998; Morse 2006) or even the population size of the larger species, in this way lessening its impact at a point high on the trophic pyramid.

Such a relationship occurs between crab spiders *Misumena vatia* (Clerck 1757) and jumping spiders (Salticidae) that frequent flowering goldenrod (*Solidago* spp.) in the late summer (Morse 2006). When *M. vatia* spiderlings emerge from their egg sacs in July and August, they are smaller than the middle-instar (± fourth instar) jumping spiders that hunt at these sites, even though late-instar and adult *M. vatia* considerably exceed these jumping spiders in size and routinely prey on them (Morse 1992). As a consequence, although both *M. vatia* spiderlings and the jumping spiders feed

on many of the same prey when in the vicinity of flowers, jumping spiders may capture *M. vatia* spiderlings in late summer and autumn. Sometimes locally abundant, *M. vatia* spiderlings may then even provide an important food source for juvenile jumping spiders, and these jumping spiders may become one of the major sources of mortality for the crab spiderlings (Morse 1992). It is therefore of considerable interest to establish whether the distribution of the two species on flowers at this time is nonrandom in relation to each other. Establishing this relationship will provide important insight into whether the presence of one species affects the distribution of the other, or whether the numbers of individuals reported in earlier studies (Morse 1992, 2006) are a mere consequence of random contacts between the two species, which may both be drawn to flowers attracting large numbers of prey insects (Morse 2000, 2005). These results have important implications for the nature and integrity of these species and for the food web in general. Here I present a series of observations and experiments that address this question.

METHODS

Site and species.—I conducted this work at the Darling Marine Center of the University of Maine, South Bristol, Lincoln County, Maine, USA, in a 3.5 ha old field surrounded by mixed coniferous-deciduous forest. The field, mown yearly in October, contains several grasses (Gramineae), and the main forbs flowering during the study period are goldenrods, asters (primarily *Aster umbellatus*) and wild carrot *Daucus carota*.

This study was confined to Canada goldenrod (*Solidago canadensis*), by far the commonest flowering species in the study area during late July and August. Canada goldenrod grows in clones that form distinct clumps in the study area. Most flowering clones contain 15–70 flowering stems of 70–100 cm height, culminating in large yellow, plume-like inflorescences with hundreds of small flower heads. Those used in this study contained 25–35 flowering stems, which I used as they reached peak flowering.

Misumena vatia spiderlings weigh 0.4–0.7 mg when they emerge from their natal nests in late summer (Morse 1993). They then move rapidly on silk lines in search of satisfactory hunting sites, usually goldenrod inflorescences, due to their ubiquity during this period and to the spiderlings' strong preferences for these flowers (Morse 2005). Throughout this paper the term "spiderling" refers exclusively to second-instar *M. vatia*. Several species of small jumping spiders, typically in their middle instars, also frequent goldenrod inflorescences in the study area. Though smaller than *M. vatia* of the same instar, and potential prey of late-instar and adult *M. vatia*, in late summer they are larger than recently emerged young *M. vatia* and readily prey on them (Morse 1992). By far the commonest of these jumping spiders is *Pelegrina* (=*Metaphidippus*) *insignis* (Banks 1892), and others include *Eris militaris* (Hentz 1845) and *Evarcha hoyi* (Peckham & Peckham 1883). All salticids used in experiments reported in this study were *P. insignis*. In a recent study at this site, *P. insignis* made up 88% of the middle-instar jumping spiders, *E. militaris* 9%, and *E. hoyi* 3% (Morse 2006).

Censuses and experiments.—I censused *M. vatia* spiderlings and jumping spiders, as well as other possible predators, on several flowering goldenrod clones. Since other possible predators were only occasionally found on these flowers (small nabid, reduviid, and phymatid bugs) I do not consider them further. I first carefully inspected each inflorescence by hand and then beat the inflorescences several times, initially gently, against a flat, hard, white surface to flush and locate any individuals not found in the initial inspection. Numbers of spiderlings and jumping spiders recorded in these censuses were compared to determine whether their numbers were correlated with each other.

I used many of the cleared goldenrod clones, randomly selected, to conduct the experiments. I placed sets of 20 *M. vatia* spiderlings, one per inflorescence, on each of 60 clones. Before releasing the spiderlings, I dusted them with fluorescent red powdered micronite dye to facilitate recapture. This treatment does not affect the behavior of the spiderlings (Morse 1993, 2000) or their vulnerability to predation (Morse 2006). One day later I censused 15 of these clones exhaustively for numbers of remaining dyed individuals and numbers of jumping spiders that had recruited to these sites. I similarly censused 15 more of these clones on days 2, 3, and 4 following the introductions.

Table 1.—Numbers of crab spiderlings (= crab) and jumping spiders (= jump) on goldenrod clones (mean ± SE). Linear regressions of numbers of the two species on individual inflorescences tested by *t*-tests (Zar 1999:336). $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $****P < 0.0001$. Number originally on inflorescences (Day 0), numbers present one to four days after clearing of inflorescences and addition of spiderlings (Days 1–4), and numbers present one to two days after clearing of inflorescences and addition of spiderlings and jumping spiders (Days 1–2).

Spiders added	Days	Clones used	Number of crab	Number of jump	r^2	*t*
0	0	37	1.8 ± 0.35	0.9 ± 0.18	−0.22	2.14*
20 crab	1	15	6.8 ± 0.95	0.3 ± 0.21	−0.47	6.05****
20 crab	2	15	6.7 ± 1.12	0.6 ± 0.32	−0.45	4.77***
20 crab	3	15	4.9 ± 0.83	0.4 ± 0.19	+0.53	6.11****
20 crab	4	15	3.2 ± 0.56	0.4 ± 0.19	+0.32	5.52**
20 crab, 3 jump	1	10	7.1 ± 0.97	1.1 ± 0.28	−0.50	5.28***
20 crab, 3 jump	2	10	5.1 ± 1.08	0.5 ± 0.27	+0.21	4.27**

I also ran similar experiments ($n = 20$ clones) in which I introduced three jumping spiders (dyed green) at the same time as the 20 *M. vatia* spiderlings. I censused 10 of these sites after 1 day and the other 10 after 2 days.

While recording data from the experimental clones, I captured as many of the jumping spiders as possible. I examined them carefully, especially their mouthparts, under a dissecting microscope for traces of dye to determine whether they had captured any of the spiderlings, or dyed jumping spiders in the case of undyed individuals. Tests had previously established that these dyes remain on their mouthparts for up to a few days after feeding on recently marked spider or insect prey (Morse 2006). This technique thus provides a convenient method for establishing minimum rates of jumping spider predation on the spiderlings in the field. The dyeing procedure also permitted me to separate the test *M. vatia* spiderlings from any other conspecifics that might have recruited to the sites subsequent to the manipulation (whose numbers were very low).

Voucher specimens were placed in the Florida State Collection of Arthropods, Gainesville, Florida.

RESULTS

Numbers of *M. vatia* spiderlings and jumping spiders were negatively related on unmanipulated goldenrod clones (Table 1). On cleared clones seeded with spiderlings, numbers of spiderlings and recruiting jumping spiders were initially strongly negatively correlated (days 1 and 2), but then suddenly became strongly positively correlated on days 3 and 4 (Table 1). A similar pattern held on the clones seeded with both spiderlings and jumping spiders; however, the transition on these clones occurred after only 1 day rather than 2 days (Table 1).

Where only spiderlings were added to the clones, there was no relationship over the four-day period between the number of jumping spiders present and whether the relationship between the two groups was negative or positive (Table 1). Jumping spiders recruited to these sites rapidly, such that their numbers (means = 0.3–0.6 per clone; totals of 5–9 individuals in 15 clones) were rather similar in each of these samples. In contrast, in the clones to which jumping spiders were added, their numbers were considerably higher on day 1 than in the clones to which only spiderlings were added. However, on day 2, numbers of jumping spiders on the "seeded" sites were similar to numbers at sites to which only spiderlings were added (Table 1).

Free-ranging spiderlings exhibited a strongly clumped distribution. Many fewer singletons and pairs and many more vacant sites occurred than predicted by chance in a Poisson distribution (Fig. 1: $G = 102.05$, $df = 3$, $P < 0.001$ in a *G*-test for goodness of fit).

Free-ranging jumping spiders at the census sites were also not randomly distributed when compared with a Poisson distribution (Fig. 2): $G = 22.29$, $df = 2$, $P < 0.001$ in a *G*-test for goodness of fit). They exhibited fewer ones and twos, and more zeros and threes, than predicted from a Poisson distribution. A particularly striking result was the abrupt drop-off between threes and fours, a factor that could not be

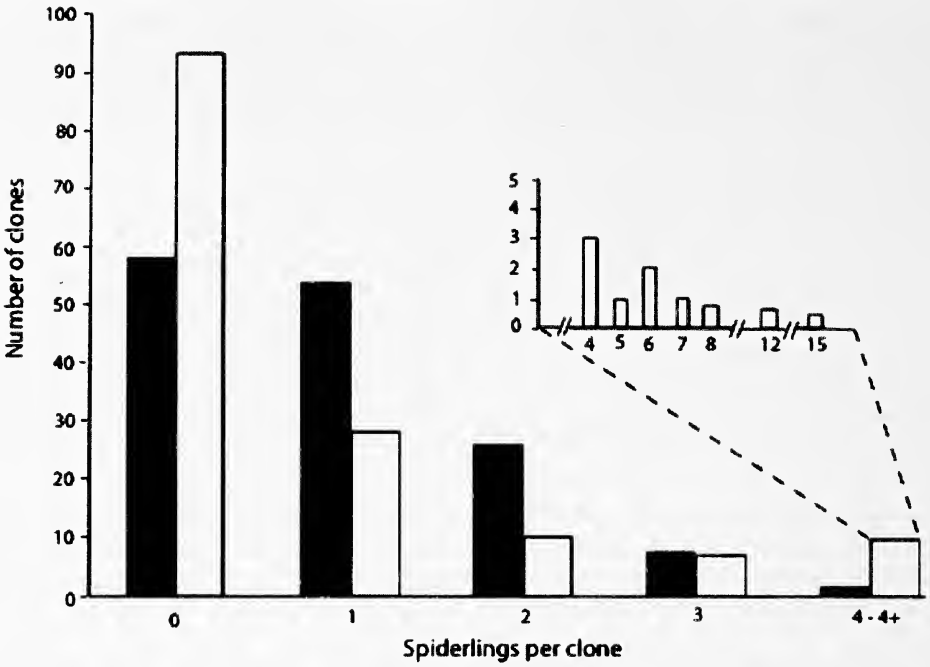

Figure 1.—Expected (black bars) and observed (white bars) numbers of *Misumena vatia* spiderlings on goldenrod clones, $n = 146$. Expected numbers based on a Poisson distribution. Inset details numbers of clones containing four or more spiderlings. Axis labels for insert are same as major figure.

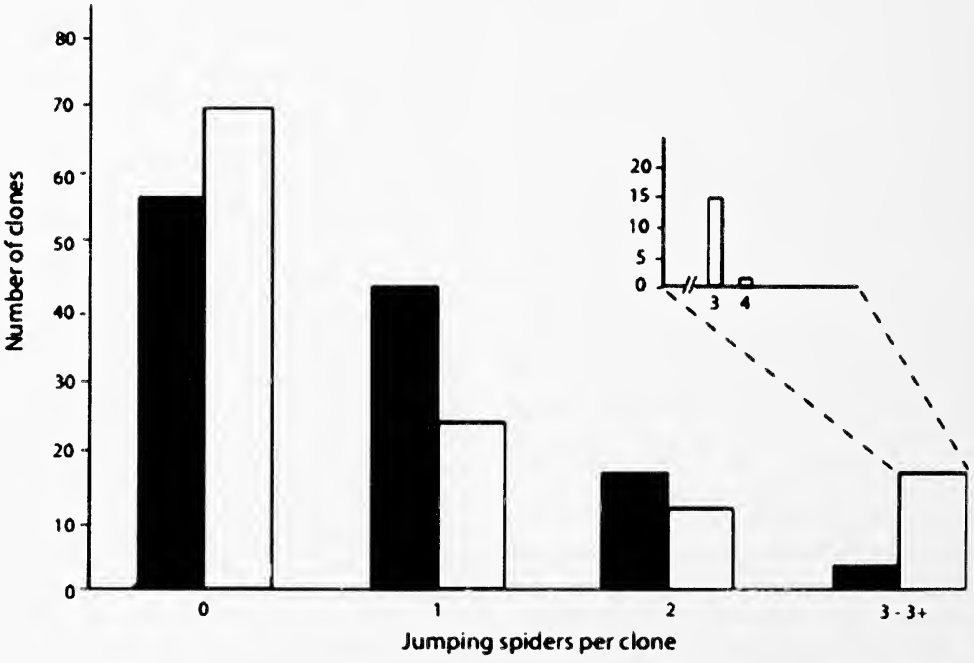

Figure 2.—Expected (black bars) and observed (white bars) numbers of jumping spiders on goldenrod clones, $n = 122$. (n does not match that of Figure 1 because data for jumping spiders were inadvertently not gathered at 24 clones.) Expected numbers based on a Poisson distribution. Inset details numbers of clones containing three or more jumping spiders. Axis labels for insert are same as major figure.

explicitly incorporated into the test for significance due to the small expected number of individuals at those densities.

In the analysis of the jumping spiders captured on the goldenrod clones, 17 of the 39 individuals (43.6%) examined contained pink dye about their mouthparts, highly suggestive of significant predation on the experimental *M. vatia* spiderlings. Only a minority of marked jumping spiders was recorded in subsequent censuses (27.3%, $n = 32$).

DISCUSSION

The free-ranging spiderlings showed a weak avoidance of the clones occupied by jumping spiders, and they exhibited a strong tendency for clumping, probably a consequence of limited dispersal from their natal sites. Many of the spiderlings were concentrated at a few sites, probably members of broods that had very recently left their natal sites. Thus, the patchiness of the spiderlings doubtlessly had a strong temporal aspect to it. The abrupt drop-off in numbers of jumping spiders after they reached a density of three per clone is consistent with a density-dependent effect limiting their numbers within these sites. As cursorial predators they probably frequently encounter each other and thus quickly attain an accurate estimate of their densities.

The experiments showed an initial strong negative relationship between the spiderlings and the jumping spiders, followed by a strongly positive relationship. This distribution is consistent with the spiderlings initially avoiding the jumping spiders, either as a consequence of direct contact with the jumping spiders or possibly with their silk. Alternatively, this relationship could result from the jumping spiders capturing the spiderlings. Spiderlings flee when in near or direct contact with jumping spiders, which readily capture them when given the opportunity (Morse 2006). Other *M. vatia* life stages respond negatively to some draglines encountered (Leonard & Morse 2006), and spiderlings might have that ability as well, though I have not tested for it.

Surprisingly, the relationship between the spiderlings and jumping spiders subsequently suddenly became strongly positive. This relationship occurred after two days in the experiment without addition of jumping spiders but after only one day in the experiment with jumping spiders added. The positive relationship seems most likely to be a similar response by both species to the substrate or to small dipteran prey. The shift in distribution could be in part a consequence of the spiderlings acclimating to the jumping spiders. Once they have located satisfactory hunting sites, the spiderlings become relatively sedentary and conceal themselves within the flower heads of the inflorescences, thereby greatly lowering their vulnerability to the jumping spiders (Morse 2006). Although one might suspect that the change in distribution resulted from a decrease in the number of jumping spiders, the jumping spiders' numbers remained relatively constant over the experiments in which none of them were added. In the experiments in which marked jumping spiders were added, relatively few of those subsequently captured or sighted were marked individuals, suggesting that the population of jumping spiders on these inflorescences is large and dynamic, with members constantly entering and leaving the clones.

Thus, these results suggest a negative relationship between the two spiders that is alleviated by the spiderlings eventually finding satisfactory hunting sites. The jumping spiders likely have an even stronger effect on this relationship when they contact the spiderlings than is suggested by the results from the censuses. Observations of these interactions demonstrated that jumping spiders would typically quit a clone before searching all of the inflorescences and that they often did not find ensconced spiderlings on inflorescences that they did search. However, when they did find spiderlings, the results were pronounced—several spiderlings were captured, and the escape responses of others were striking. Escaping spiderlings quickly descended from their sites on silk lines and sprinted off into the litter (Morse 2006). Although these data suggest a low level of search activity on the part of the jumping spiders at any given time, given their strong perceptual abilities (Jackson & Pollard 1996) and the density of the spiderlings, they could be pursuing an optimal search pattern.

The tables were turned in the relationships between adult *M. vatia* and the jumping spiders in which the adults readily attacked and captured the jumping spiders (Morse 1992). Rypstra & Samu (2005) described an analogous relationship between two species of wolf spider (Lycosidae) in which late instars or adults of

Pardosa milvina (Hentz 1844) (adults = ca. 20 mg) were in regular contact with early instars of *Hogna helluo* (Walckenaer 1837) (adults = ca. 800 mg). Under these circumstances, older individuals of the small species routinely attacked the early instars of the large species, whereas most instars of *H. helluo* preyed upon *P. milvina*. Such relationships are probably not unusual.

These fluctuating relationships between major participants in the plant-pollinator system have interesting potential consequences for the organization of their communities. The jumping spiders presumably lower the impact of the crab spiderlings, which in turn take large numbers of small flies that probably function as nectar robbers (Morse 2005). The jumping spiders themselves probably capture many more small flies than they do spiderlings. It remains to be seen whether these interactions play an important role in the evolution of plant-insect relationships on goldenrods, old-field dominants. Observations suggest that in some years, numbers of *M. vatia* spiderlings in the study area are more likely to be driven by herbivores that impact the abundance of the goldenrods (bottom-up effects) (Carson & Root 2000; Morse 2007) than by predators such as small jumping spiders (top-down effects).

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RESPIRATORY REFINEMENTS IN THE MYGALOMORPH SPIDER *GRAMMOSTOLA ROSEA* WALCKENAER 1837 (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. In this study we hypothesized that *Grammostola rosea* Walckenaer 1837, an active predator of large size that depends on its two paired book lungs for respiration, would have a refined low energy strategy based on its thin air-hemolymph barrier. The morphology of book lungs and the oxygen consumption at 20° and 30° C under normal and starvation conditions were studied. The oxygen consumption was low compared to that expected for spiders from the allometric relationship, 0.027 ± 0.01 ml O_2 g^{-1} h^{-1} (average ± standard deviation), and it was depressed at 30° C under starvation. The harmonic mean thickness of the air-hemolymph barrier was 0.14 ± 0.03 μm, the respiratory surface density was 122.99 ± 35.84 mm^{-1}, and the book lung volume ranged from 12.2 to 37.5 mm^3. With these parameters a high oxygen diffusion capacity was estimated. The combination of low resting oxygen consumption and high pulmonary oxygen conductance results in very low gradients of partial oxygen pressures across the air-hemolymph barrier (0.12–0.16 kPa) required to satisfy the resting oxygen demands.

Keywords: Oxygen consumption, book lungs, mygalomorph spider

In mygalomorph spiders, respiration involves the movement of gases across an exchange surface and their combination with the circulating respiratory pigment hemocyanin (Anderson & Prestwich 1982). The book lungs are two paired organs located within the abdomen of spiders in an inextensible chitinous cavity called the atrium (Foelix 1996). The respiratory organ is composed of a series of flattened air-filled cuticular plates, the lamellae, which are projected into a hemolymphatic sinus. Gas exchange occurs across a thin cuticle-hypodermis barrier separating the gases of the atrium from the hemolymph. The book lungs constrain oxygen consumption in spiders, which exhibit resting metabolic rates about half those measured for other poikilothermic animals of equal mass (Anderson 1970; Greenstone & Bennett 1980). This low oxygen consumption has been considered an unusual energetic adaptation of sit and wait predators. Their metabolic performance is improved further by an ability to depress metabolic rates below usual resting levels during transient periods of starvation (Ito 1964; Miyashita 1969; Nakamura 1972; Anderson 1974; Humphreys 1977).

Several studies have attempted to relate foraging styles to oxygen consumption (Carrel & Heathcote 1976; Angersbach 1978; Greenstone & Bennett 1980; Paul et al. 1987; Strazny & Perry 1984; Schmitz & Perry 2001). The active jumping spider *Salticus scenicus* (Salticidae) only requires an air-hemolymph PO_2 gradient between 0.22 to 0.26 kPa for a sustained metabolic rate value of 0.312 ml O_2 g^{-1} h^{-1} at rest.

In this study we hypothesized that *Grammostola rosea* Walckenaer 1837, an active predator of large size which depends entirely on its two paired book lungs, has a low energy strategy based on large respiratory surface area and a thin air-hemolymph barrier.

METHODS

Six adult individuals of *G. rosea* (Body mass = M_b = 18.5 ± 6.2 g) were kept in individual containers for 7 days at natural lab temperatures to ensure acclimation conditions prior to measurements. Water was periodically added to a cotton swab placed at the end of the cage. Several larvae of *Tenebrio molitor* were added daily as an *ad lib.* source of food. The photoperiod was kept at 12 h:12 h L:D. After 2 wk metabolic rate (MR) was measured at 20° and 30° C. The same measurements were repeated after 3 wk of starvation.

All metabolic trials were performed during the day, which corresponds to the resting phase in this species. Rates of oxygen consumption ($\dot{V}O_2$) were used as a measure of MR, and were determined using "closed system" metabolic chambers (Vleck 1987). Animals were weighed to the nearest mg on an analytical balance and then placed individually inside a chamber of 60 cm^3. Small granules of CO_2-absorbent Baralyme™ and water absorbent Drierite™ were added to each chamber in a compartment isolated from the spider. The chambers were sealed from the atmosphere and placed for 2 h in a temperature and light controlled incubator during the resting phase. Three blank chambers served as controls for each series of measurements. After two hour long experiments we injected the air from each chamber into a Tygon™ tube connected to the O_2 analyzer. At the end of the measurement interval O_2 concentrations were determined using an Oxygen Analysis System FC 10a (Sable System International, Henderson, NV, USA), supplied with barometric pressure compensation. Output from the analyzer was recorded by a computer using EXPEDATA program (Sable's data acquisition system). Rates of oxygen consumption were calculated using:

$$\dot{V}_{O2} = \frac{V \cdot (FI_{O2} - FE_{O2})}{(1 - FE_{O2}) \cdot t},$$

where V is the initial volume of dry, CO_2-free air in the chamber at STP, FI_{O2} and FE_{O2} are the O_2 fractions within the chamber at the start and the end of incubation, respectively, and t is the duration of incubation. Comparisons among oxygen consumption at different temperatures and at the two experimental feeding conditions were performed using non parametric two-way ANOVA (Friedman test).

Three of the spiders (M_b = 13.4 ± 2.65 g) were sacrificed, and their book lungs were carefully extracted and immersed in 2.3% glutaraldehyde in phosphate buffer at 4° C for a minimum of 2 h. Next, tissues were processed for routine electronic transmission microscopy. Briefly, two randomly chosen pieces were obtained from each book lung. The pieces were washed with buffer and post-fixed with 1% osmium tetroxide for 1 h at 4° C. Tissues were then dehydrated in graded concentrations of alcohol and infiltrated and embedded in epoxy resin constructing cubes of 2–3 mm^3 that were sectioned in semi-thin sections of 1 μm. Tissue samples were stained with 1% toluidine blue. Ultra thin sections of 60–90 nm of thickness were made and mounted on copper mesh grids. These sections were contrasted with Pb-citrate. The semi-thin sections were contrasted with hematoxiline-eosine. Sections were studied using optical and transmission electron microscopy (JEOL/JEM 100SX). Six sections were photographed, digitized and six semi-thin and six ultra-thin sections per individual were analyzed using Scion Image Software. The total harmonic mean thickness of the air-hemolymph barrier (τ_h (μm)) and those of the cuticle and hypodermis layers were estimated by a stereological method in a square lattice grid as suggested by Weibel (1970/71) and Maina (2002):

$$\frac{1}{\tau_h} = \frac{3}{2} \cdot \frac{\sum_{j=1}^{m} f_j \cdot \frac{1}{l_j}}{\sum_{j=1}^{m} f_j},$$

where l_j is the mid-value of intercept length of linear probes, f_j the frequency of class j and m the number of classes.

The respiratory surface density (RS_d (mm^{-1})), the respiratory surface area (mm^2) per lung volume unit (mm^3), was estimated by means of line-intersection stereological method (Weibel 1970/71):

$$RS_d = \frac{2N}{1/2 \cdot P_T \cdot Z},$$

where N is the number of intersections between line probes of length Z with the respiratory surface and P_T is the number of testing points.

Two spiders (M_b: A1 = 13.62 g; A2 = 16.8 g) were selected to estimate the volume of the book lung (i.e., respiratory zone of the atrium). These spiders were killed and then the entire opisthosoma was extracted, fixed and contrasted. Equidistant semi thin sections of 6 μm were taken along the entire lung zone. Each section was observed and photographed under a light microscope. Each image was analyzed, determining the sectional area of the respiratory zone (Ai), and then, the total volume (BLV) was estimated based on the Cavalieri principle (Howard & Reed 2005), using:

$$BLV = \sum_i A_i \cdot d_i,$$

where d_i is the distance between the sections, and in our case a constant value of d_i = 6 μm.

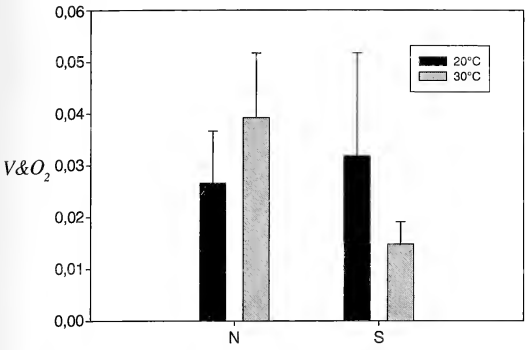

Figure 1.—Resting metabolic changes of *Grammostola rosea* at 20° (black bars) and 30° C (white bars), under normal (N) and starvation (S) conditions. $\dot{V}O_2$ = oxygen consumption (ml O_2 h^{-1} g^{-1}). Means + 1 SD are shown.

From those values the oxygen diffusion capacity (D_tO_2) that represents the oxygen conductance of each layer of the air-hemolymph barrier was estimated by:

$$DO_i = \frac{\kappa \cdot RS_d \cdot BLV}{\tau_h},$$

where DO_i is the oxygen diffusion capacity of a layer and κ is the Krogh's diffusion coefficient: 1.28×10^{-8} cm^2 min^{-1} kPa^{-1} ($= 76.8 \times 10^{-8}$ cm^2 h^{-1} kPa^{-1}) for the cuticle and 2.05×10^{-7} cm^2 min^{-1} kPa^{-1} ($= 123.0 \times 10^{-8}$ cm^2 h^{-1} kPa^{-1}) for hypodermis (Schmitz & Perry 2001). Because the oxygen conductance is the inverse value of the resistance (D_tO_2 = 1/R), and cuticle and hypodermis are disposed in a series array, the total D_tO_2 of both layers was computed by:

$$\frac{1}{D_tO_2} = \frac{1}{DO_c} + \frac{1}{DO_h},$$

where DO_c and DO_h are the oxygen diffusion capacities of the cuticle and hypodermis, respectively. Finally, the required gradient of oxygen partial pressures between the gases of the atrium and the hemolymph for a particular value of oxygen consumption ($\dot{V}O_2$*) was estimated by $\Delta PO_2 = \dot{V}O_2*/D_tO_2$.

RESULTS

Grammostola rosea showed a low $\dot{V}O_2$ at 20° C, 0.027 ± 0.01 ml O_2 g^{-1} h^{-1}, with a Q_{10} = 1.65 ± 0.78 between 20° and 30° C of environmental temperature. The metabolic rate was affected by the different conditions (χ^2_3 = 9.72, P = 0.02) and this was due to a decrease in $\dot{V}O_2$ at 30° C in the starvation condition (P < 0.05 in planned comparisons) and marginally due to the temperature factor (P = 0.07; Figure 1).

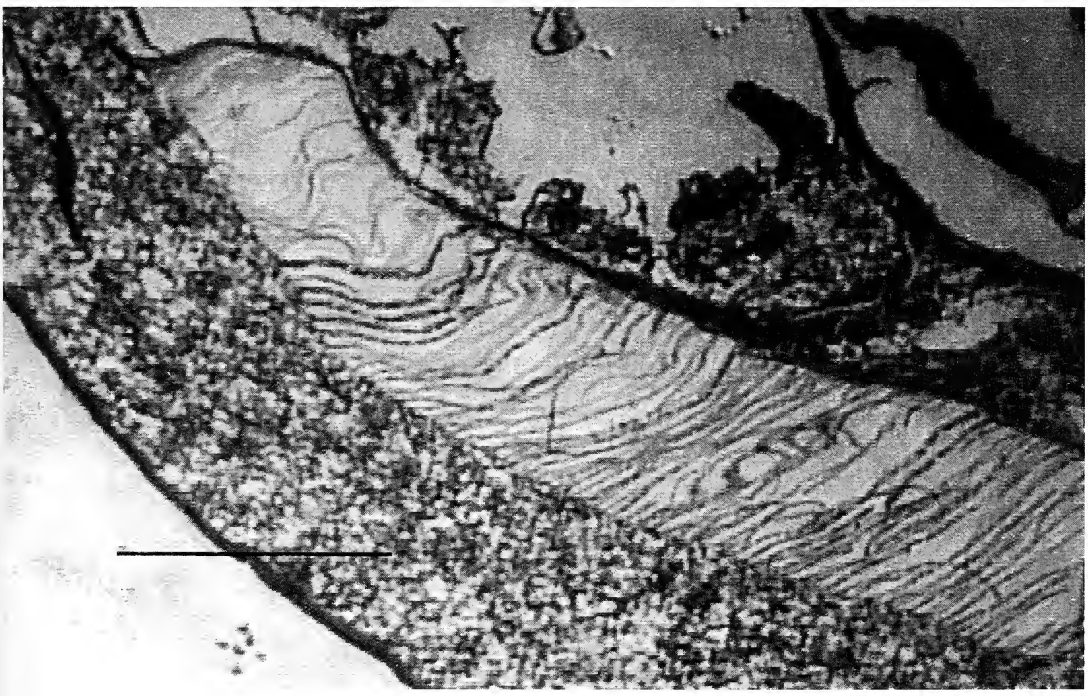

Figure 2.—Semi thin section of the book lung of *Grammostola rosea* (10×). Scale bar = 1 mm.

Table 1.—Metabolic and structural respiratory parameters in two spiders, *Grammostola rosea*. M_b = body mass, $\dot{V}O_2$ = oxygen consumption at 20° C, BLV = book lung volume, D_tO_2 = oxygen diffusion capacity, $DtO2^m$ = mass-specific oxygen diffusion capacity, and ΔPO_2 = required gradient of partial oxygen pressures between air and hemolymph to support these $\dot{V}O_2$ values.

Spider	M_b (g)	$\dot{V}O_2$ (ml O_2 h^{-1} g^{-1})	BLV (mm^3)	D_tO_2 (cm^3 h^{-1} kPa^{-1})	$D_tO_2{}^m$ (cm^3 h^{-1} kPa^{-1})	ΔPO_2 (kPa)
A1	13.62	0.0372	12.2	3.165	0.233	0.160
A2	16.8	0.0659	37.5	9.277	0.552	0.119

The respiratory surface density was RS_d = 122.99 ± 35.84 mm^{-1} and the harmonic mean thickness of the air-hemolymph barrier was τh = 0.14 ± 0.03 µm (Fig. 2). The cuticle represents 22.2 ± 10.3% of the total thickness of the barrier. The book lung volume of the spiders A1 and A2 were 12.2 mm^3 and 37.5 mm^3, respectively. Their respiratory surface area ($RS_d \times BLV$) was estimated to vary between 1500.5 mm^2 to 4612.1 mm^2. These spiders showed a $\dot{V}O_2$ = 0.037 ml O_2 h^{-1} g^{-1} and $\dot{V}O_2$ = 0.066 ml O_2 h^{-1} g^{-1} at 20° C. Considering these values, oxygen diffusion capacities for the cuticle 3.85 cm^3 h^{-1} kPa^{-1} and 11.28 cm^3 h^{-1} kPa^{-1}, and oxygen diffusion capacities for the hypodermis 17.86 cm^3 h^{-1} kPa^{-1} and 52.24 cm^3 h^{-1} kPa^{-1} were obtained for A1 and A2 spiders respectively. The oxygen diffusion capacities of the total barrier (D_tO_2) are given in Table 1.

DISCUSSION

Grammostola rosea showed refined morphological characteristics in its book lungs. Their thin air-hemolymph barrier, combined with appropriate values of respiratory surface density and book lung volume, results in high oxygen diffusion capacities allowing a good oxygen delivery even at low oxygen pressures.

The respiratory surface area of *G. rosea* was lower than that reported for *Aphonopelma* (*Eurypelma*) *californicum* {(Ausserer 1871) Theraphosidea, nomina dubium (Platnick 2006)} (6400 mm^2; Focke 1981). Compared with other spiders, the RS_d was lower than that for the jumping spider *Salticus scenicus* (Clerck 1757) (Salticidae) and lower than *Tegenaria* spp. (Agelenidae) 210–250 mm^{-1} and 355–390 mm^{-1}, respectively. However, the thickness of the air-hemolymph barrier in *G. rosea* (0.14 µm) was thinner than that of these spiders, 0.17–0.18 µm in *S. scenicus* and 0.4 µm reported in *Tegenaria* spp. (Strazny & Perry 1984; Schmitz & Perry 2001). The resulting D_tO_2 (0.233 cm^3 h^{-1} kPa^{-1}) was similar to that of *Tegenaria* spp. 0.258–0.552 cm^3 h^{-1} kPa^{-1} but lower than that of *S. scenicus* 0.720–0.984 cm^3 h^{-1} kPa^{-1}. The required gradient of partial oxygen pressures between air and hemolymph to support the resting $\dot{V}O_2$ at 20° C (ΔPO_2) was 0.119 to 0.160 kPa, which is close to the required 0.22–0.26 kPa required by *S. scenicus* at rest (Schmitz & Perry 2001). The lower ΔPO_2 requirement of *G. rosea* compared with that of *S. scenicus* in spite of their lower D_tO_2 arises from its lower mass specific oxygen consumption and represents a value of about 2% of that reported in mammals (7.5 kPa). The required $\Delta PO2$ in *G. rosea* is also lower than 0.7 kPa, a value estimated across the lung barrier in *Aphonopelma californicum* during rest (Angersbach 1978; Paul et al. 1987). Considering that spiders have aerobic scopes between 5 and 8 (Seymour & Vinegar 1973; Herreid 1981; Anderson and Prestwich 1985), the ΔPO_2 required by an active individual of *G. rosea* could reach 0.8 kPa and a maximum of 1.28 kPa. A required ΔPO_2 = 7 kPa was estimated across the walls of the lungs of *A. californicum* after activity (Angersbach 1978; Paul et al. 1987), a value near those usually found in mammals; however this estimation was performed assuming a thick air-hemolymph barrier (0.89 µm). If we replace that value by 0.2 µm, similar to *G. rosea* and other spiders, the required ΔPO_2 decreases to 1.59 kPa, similar to our result. Our results are lower but comparable to the range of 2.2 to 3.0 kPa estimated for the active jumping spider *S. scenicus* and the 2.4 kPa measured in the less active *Tegenaria* spp. during molting.

Grammostola rosea showed 63.3% of the expected oxygen consumption for spiders from the allometric relationship: log $\dot{V}O_2$ (µL h^{-1}) = −0.133 + log M_b (mg) (Greenstone & Bennet

1980), less than half of the values measured for other poikilothermic animals (Anderson 1970). The value of $\dot{V}O_2$ is similar to those of *Aphonopelma eutylenum* Chamberlin 1940 (Theraphosidae) (0.018 ml O_2 h^{-1} g^{-1}; Greenstone & Bennet 1980) and *A. californicum* (0.013 ml O_2 h^{-1} g^{-1}; Paul et al. 1987). Moreover, *G. rosea* showed depressed metabolic rates after a starvation period of three weeks, agreeing with results from other spiders (Ito 1964; Miyashita 1969; Nakamura 1972; Anderson 1974; Humphreys 1977). This metabolic depression was only evident at 30°C, probably due to the high energetic requirement derived from the exponential relationship between temperature and metabolism in ectothermic animals.

In Chile there are no studies on the population dynamics of this species but it is possible to find adults throughout the year. The reported metabolic and morphologic findings could account for a general lack of numerical responses to insect prey availability in this temperate zone (Greenstone 1978) and could be part of physiological adaptations to tolerate low or unpredictable food availability (McNab 1974), buffering spiders against the environmental fluctuations (Mediterranean weather) characteristic of their habitat in central Chile.

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JUMPING SPIDERS ASSOCIATE FOOD WITH COLOR CUES IN A T-MAZE

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ABSTRACT. Salticid spiders are a tractable group for studies of learning. We presented *Phidippus princeps* Peckham & Peckham 1883 with the challenging task of associating prey with color cues in a T-maze. Experimental spiders were given the opportunity to learn that a cricket was hidden behind a block of a particular color. To eliminate the use of other cues, we randomly assigned both block position within the maze, and maze location within the room. For control spiders, no cues predicted the location of prey. We gave spiders two blocks of trials. Each block consisted of four training trials followed by a probe trial in which no prey was present. Trials lasted an hour, and spiders were given one trial per day. Not all spiders were successful in finding the prey during training trials. In the first probe trial, there was no evidence of learning: there was no effect of treatment, the number of successful training trials, or their interaction on which block the spiders chose first. In the second probe trial, there was a significant interaction between treatment and number of successful training trials: experimental-group spiders with a greater number of successful training trials were more likely to choose the correct block in the probe trial. This study demonstrates that *P. princeps* can learn the location of prey by color cues alone, a challenging task, and adds to the growing literature on learning in spiders.

Keywords: Learning, experience, *Phidippus*, Salticidae, vision

In spite of their small brain size, many spider species are capable of modifying their behavior with experience. Experience influences behavior in many aspects of spiders' lives, including mate choice (Hebets 2003), foraging (Jackson & Wilcox 1993; Sebrier & Krafft 1993; Edwards & Jackson 1994; Punzo 2002a, b; Punzo & Ludwig 2002; Nakata et al. 2003), antipredator behavior (Punzo 1997), locomotory behavior (Punzo & Alvarez 2002) and intraspecific conflict (Whitehouse 1997; Dodson & Schwaab 2001; Hoefler 2002).

Jumping spiders (Araneae, Salticidae) are an exceptionally good model system for studying learning. They are renowned for the visual acuity of their anterior median eyes (Land & Nilsson 2002), so visual stimuli are likely to be salient and easily sensed. Visual stimuli are also relatively easy to standardize compared to other sensory modalities such as odor, so this system is particularly tractable experimentally.

Jumping spiders have been shown to be able to learn in several different contexts. Most species are generalist predators, so it would be beneficial to have the ability to learn to avoid dangerous or distasteful prey, or to select beneficial prey. Even when prey toxins are not fatal, predators that feed repeatedly on them may sicken and grow more slowly (Paradise & Stamp 1991; Strohmeyer et al. 1998; Toft 1999). Salticid species do indeed learn during foraging. For example, with experience, *Phidippus regius* Koch 1846 improve in their ability to capture palatable prey and decline in their tendency to attack ants. Naive *P. princeps* Peckham & Peckham 1883 readily attack milkweed bugs, but learn to avoid them after repeated exposures (Skow & Jakob 2006).

Learning also has clear fitness consequences during navigation. *Phidippus* spp., like many other jumping spiders, construct a silken nest for protection during the night, in inclement weather, and during egg guarding (Jackson 1979). Spiders often forage away from their nests during the day, but return to them at dusk. *Phidippus clarus* Keyserling 1885 apparently attends to cues near its nests in order to locate it again: spiders that had nests on wooden dowels were more likely to approach novel dowels of the same color than were either spiders with no experience with dowels, or with experience only with dowels of a different color (Hoefler & Jakob 2006).

We presented *Phidippus princeps* with the task of moving through a simple maze in order to find prey associated with a cue of a particular color. Only cue color and not its location predicted the location of prey. This task was potentially challenging: in nature, rewards may be associated with reliable cues (e.g., nest sites associated with particular structural characteristics, or prey associated with flowers or dung pats), but the cues are likely to be stable in location. However, Hoefler & Jakob's (2006) experiment, described above, demonstrated that *P. clarus* can recognize nest sites based solely on color cues: spiders had equivalent levels of response to familiar beacons (both color and location cues present) and novel beacons of the same color (color cues present but location cues absent). We were interested in whether the spiders could learn a similar task in the context of foraging.

A second feature of the current experiment is that we gave spiders only a single training trial per day, so they were required to remember the association for a long period. Again, this makes this a challenging task, but perhaps this time delay between training trials is similar to what foraging spiders encounter in nature. Given that *P. princeps* live in heterogeneous habitats with patchily-distributed prey and vegetation types, spiders may not encounter a particular pairing of prey with a particular environmental feature very frequently.

METHODS

Spider collection and maintenance.—We captured *P. princeps* spiders by sweep netting fields with a mixture of grasses and wildflowers in Amherst, MA, in the fall of 2003. Voucher specimens have been placed in the entomology collection at the University of Massachusetts Amherst. We kept spiders individually in ventilated plastic cages, either 23 × 31 × 10 cm high or 13.5 × 19 × 9.5 cm high, and provided ad libitum water and 4–6 crickets weekly. Each cage contained a painted green stick and leafy plastic vines to encourage normal spider behavior (Carducci & Jakob 2000). The daily light cycle was 14L:10D.

Testing.—The apparatus and procedure closely followed Popson (1999). Adult females were tested during winter 2003–04. We constructed T-mazes of 6 mm thick Plexiglas. The entry arm of the maze was 30 cm long, and the top of the T measured 40 cm from tip to tip. All arms were 10 cm wide × 10 cm high. We covered the outside walls with white contact paper to reduce visual cues from the room. A thin film of petroleum jelly lining the bottom of the inner walls discouraged spiders from climbing.

Cues were wooden cubes 3.2 cm on a side, painted either red or blue (Aleene's Premium Coat Acrylic, True Red: reflectance peak at 700 nm; Deep Blue: reflectance peak at 450 nm). These colors were chosen because spiders could distinguish similar colors in a previous experiment (Popson 1999). Colors were not matched for saturation or brightness. We coated the blocks in petroleum jelly to discourage spiders from climbing on them. We placed one block at each end of the top of the T, 5.5 cm from the end wall. The reward was a live cricket secured with nontoxic glue to a small piece of index card. In preliminary tests, spiders readily fed on crickets prepared in this way. Spiders could see the cricket only by walking behind the block.

We randomly assigned 55 spiders to either a control or experimental group. In the control group's training trials, prey were placed randomly with respect to both side of the maze (left or right) and color of block (red or blue). In the experimental group, prey were placed randomly with respect to side, but were always behind the same color block. The rewarded color was assigned randomly for each individual. For both groups, location of the maze was assigned randomly for each trial, so that room cues (such as direction of the light source or appearance of the ceiling) did not indicate prey location. Thus, for the experimental group, only block color predicted prey location, and for the control group, no cues predicted prey location.

We placed mazes on top of a layer of sand inside a 2-m^2 arena. The sand reduced vibrations that may have disturbed the spiders. Seven mazes were run simultaneously. We released spiders into the mazes via a 20 ml, 2-cm diameter open-topped syringe, covered with opaque tape. We placed a spider into a syringe, blocked the top with a cotton ball wrapped in a tissue, and inserted the syringe into a hole drilled through the wall in the center of the bottom of the T. Between trials, syringes and mazes were washed with soapy water, sprayed with alcohol and wiped dry to disrupt any chemical cues left by previous spiders. Fresh cotton plugs were used for each trial.

Spiders were allowed to acclimate in the syringe for 5–8 min before the start of the trial. We then started the video camera mounted above the mazes, moved to the first maze, removed the cotton ball, and slowly pushed the syringe plunger flush with the inner wall of the maze. We moved swiftly from maze to maze so that all trials began within 2 min, and then left the room so that spiders were not disturbed. Trials were terminated after an hour, and spiders were removed from their mazes in the same order in which they were put in. Review of videotapes revealed that no spider finished feeding on a prey prior to the end of the hour.

We tested spiders once per day for 10 consecutive days between 10:00 and 15:00 h. Days 1–4 and 6–9 were training trials, and prey were present in the maze. Days 5 and 10 were probe trials with the same procedure but with no prey in order to eliminate the effect of odor or sound cues from the prey on the spiders' choices.

Not all spiders captured prey during training trials, so not all spiders had equal opportunity to learn the task. We scored a training trial as successful if the spider fed on the prey. For experimental spiders, we scored a probe trial as correct if the spider walked behind the rewarded block first. For control spiders, at the start of the experiment we randomly assigned a block color for each spider. We scored a probe trial as correct if the spider walked behind the randomly assigned block. We chose this method instead of assigning a particular color to be correct in case spiders were more likely to favor a particular color; however, the analyses generated indistinguishable results.

Analysis.—We used logistic regression, with the choice of block in the test trial as the dependent variable. We tested three independent variables: treatment group, the number of successful training trials (a continuous variable), and their interaction. If experience influences choice in the probe trial, spiders in the experimental group, where color predicted prey location, should improve with higher numbers of successful training trials. In control spiders, there should be no relationship between the number of successful trials and choice in the probe trial. Thus, we expected a significant interaction term if learning took place.

RESULTS

There was no effect of treatment, training, or their interaction on the outcome of the probe trial on Day 5 (Table 1). Thus, we have no evidence that spiders learned the association in the first four training trials.

Approximately equal numbers of spiders in the control and experimental groups chose the correct block in Trial 10 (control: 10 of 22; experimental: 13 of 23). However, there was a significant interaction between training success and group: the number of successful training trials (out of a total of eight training trials) increased the probability of experimental spiders finding the prey in the test trial, but not that of control spiders (Fig. 1; Table 1). Another way to examine this question is to compare the number of successful training trials for spiders that made correct vs. wrong choices. Experimental spiders that made the correct choice in probe Trial 10 had significantly more successful training trials than spiders that made the wrong choice (unpaired t-test; $t = 2.339$; $P < 0.03$; mean $\pm$ SE, correct: 5.5 ± 0.49, incorrect: 3.7 ± 0.63). However, there was no difference for control spiders ($t = -1.291$; $P = 0.19$, correct: 3.0 ± 0.63; incorrect: 4.3 ± 0.71).

DISCUSSION

Phidippus princeps jumping spiders were significantly more likely to look behind a block that visually predicted the presence of prey when they had an adequate number of successful training trials to gain this experience. Spiders showed no evidence of learning after four training trials, and even after eight training trials a substantial number of spiders made the wrong choice in the probe trial.

Table 1.——Success of spiders in probe trials on days 5 and 10. For probe trials on Day 5, there was a maximum of four successful training trials. For probe trials on Day 10, there was a maximum of eight successful training trials.

	df	Likelihood Ratio χ^2	*P*
Probe trial on Day 5			
Group (control vs. experimental)	1	0.620	0.43
Number of successful training trials	1	2.515	0.11
Group × number of successful training trials	1	0.205	0.65
Probe trial on Day 10			
Group (control vs. experimental)	1	0.261	0.61
Number of successful training trials	1	0.680	0.41
Group× number of successful training trials	1	6.661	0.01

Jumping spiders have UV, green, and possibly blue and even red-sensitive cells in the retina of their anterior median eyes (reviewed in Lim & Li 2006). Thus, it is possible that our spiders used hue to distinguish between the red and blue cues that we presented. However, because we did not control for brightness or saturation of our color cues, we cannot be certain that spiders relied solely on hue.

The learning task was particularly difficult for a number of reasons. First, because of the length of time required for each trial, we ran multiple trials simultaneously. In order to avoid disturbing spiders, we left all spiders in their mazes for one hour rather than removing them after they made their initial choices. This meant that a spider could make an incorrect choice, and indeed spend much of its time on the unrewarded side of the maze, but then make the correct choice and capture the prey. Thus, the strength of the relationship between the stimulus and the reward was low. In contrast, in a number of other studies, spiders were given more extensive experience with the task to be learned (e.g., Punzo 2002a; Punzo & Preshkar 2002; Hoefler & Jakob 2006).

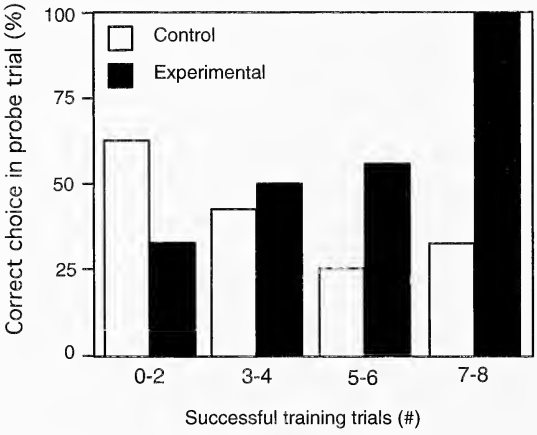

Figure 1.—The—percentage of *Phidippus princeps* that chose the correct block in the second probe trial after two blocks of four training trials. Not all spiders successfully found and attacked the prey on all training trials. For the experimental group, where prey were always hidden behind the same color block, increased success in training trials led to better performance at the probe trial. There was no relationship for control spiders, for which no cues consistently predicted the location of prey.

This learning task was also difficult because the time between the final training trial and the probe trial was quite long (24 h). In most controlled studies of associative learning in spiders, only much shorter retention periods have been examined. For example, Skow & Jakob (2006) trained spiders to avoid aversive prey, and then tested them 50 min after their final training trial. In another experiment, Skow (2007) gave spiders a series of electric shocks paired with a set of visual cues. Five min after the completion of the training session, spiders were given a choice between shock-associated cues and another set, and significantly more often chose the new set. Nakamura & Yamashita (2000) trained jumping spiders (*Hasarius adansoni* Audouin 1826) to avoid the heated side of a small dish over a three-min session, and tested them immediately after training. Rodríguez & Gamboa (2000) found that three web-building species form memories of captured prey, and return to search for stolen prey soon after it was removed from the web. Tarantulas learned to avoid shock by raising their legs, and retained this memory for an hour (Punzo 1988). There are, however, some studies that examined longer retention

periods. For example, Hebets (2003) demonstrated that female wolf spiders (*Schizocosa uetzi* Stratton 1997) exposed to courting males as subadults prefer males of the same phenotype when tested 11 days later or more after they had molted to maturity. Punzo (1997 and pers. comm.) found that wolf spiders (*Schizocosa avida* Walckenaer 1837) avoided scorpion cues 48 h after a negative encounter with a scorpion. Research that methodically examines the rate of acquisition of learned associations and the rate of decay of these memories would be especially valuable in understanding the extent to which spiders rely on learning in their daily lives.

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SOCIAL ENCOUNTERS BETWEEN MALE BROWN SPIDERS, *LOXOSCELES GAUCHO* (ARANEAE, SICARIIDAE)

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ABSTRACT. Twenty-two interactions between males of *Loxosceles gaucho* Gertsch 1967 were investigated in order to study its intrasexual interactions and level of aggressiveness. Aggression by lunges or bites was observed in just 22.7% of the trials and three behaviors were identified as aggression-attenuating mechanisms: a hug; fleeing, and a postural pattern (POS). Interactions took place in 59.1% of the trials and the pairs interacted using one or two behavioral patterns (vibratory and/or postural). The vibratory pattern (VIB) consisted of foreleg vibration, palpal drumming, and abdominal pulsation and was used by both resident and intruder opponents. The postural pattern (POS) was used exclusively by resident males and it was similar to the behavioral pattern of sexually receptive *L. gaucho* females; in these cases the intruder male responded using the VIB. In conclusion, the interaction between adult *L. gaucho* males is usually non-aggressive. The behaviors described in this study possibly promote group-living and help to explain the gregarious populations of recluse spiders. Intra-specific sexual mimicry can occur in these interactions, but this hypothesis requires further investigation.

Keywords: Aggression, gregariousness, male-male interaction, sexual mimicry

Aggression takes place when an animal attacks or threatens an opponent. Findings in Game Theory have shown that aggressive or agonistic encounters between conspecifics usually minimize and/or delay aggression, improving the individual fitness of the opponents (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Whitehouse 1997). In male-male spider interactions, some particular characteristics or behaviors can act as aggression-attenuating mechanisms, such as differences in weight (Suter & Keyley 1984) or size (Whitehouse 1997; Bridge et al. 2000; Taylor & Jackson 2003), and ritualized behaviors (Lubin 1986). Even the presence/absence of determined elements in the contest area can affect opponent aggressiveness, as shown by Wells (1988) for male *Trite parvula* (Bryant 1935) (Araneae, Salticidae), which escalate contests in the presence of a female model.

In addition, aggressiveness and tolerance are key factors to understand the evolution of social behavior in spiders (see Uetz & Hieber 1997). Most spiders are essentially solitary, but a few species have different degrees of sociability that range from aggregations of individual webs to cooperative brood care (Avilés 1997). There are species that exhibit social plasticity, i.e., that do not display obligatory social behavior. These species are a primary animal model for the study of aggression-attenuating mechanisms. This is the case of the recluse spiders that are generally solitary but can aggregate around and inside buildings (Bücherl 1961; Horner & Stewart 1967; Fischer & Vasconcellos-Neto 2005; Marques-da-Silva et al. 2006).

Individuals of the recluse spider *Loxosceles gaucho* Gertsch 1967 (Araneae, Sicariidae) are usually solitary in their natural habitat, as in the Butantan Institute woods (Japyassú et al. 2003). However, like other recluse spiders they aggregate in manmade environments or in disturbed natural habitats. For instance Stropa & Pinhal (2005) found adult *L. gaucho* aggregating in brick piles deposited on the ground; and Stropa (2004) reported that two males of this species may share a small retreat in the field during the day. At night, however, males commonly wander searching for females. The silk produced by both males and females is easily recognized in the field and is abundant, at least in the Botanic Garden from Botucatu, Brazil. The silk covers portions of the spiders' retreats which are mainly in crevices and the cavities of the litter. The web of *L. gaucho* is thin, white, and irregular and covers the substrate like a thin sheet. *L. gaucho* also occurs in house yards but there is no evidence that it prefers this habitat (Stropa & Pinhal 2005). It is

endemic from southwestern Brazil and it occurs mainly in the states of São Paulo and Paraná (Marques-da-Silva & Fischer 2005).

In this study, a resident-intruder paradigm was used to examine interactions between male *L. gaucho* in order to study its intrasexual aggressiveness and to explore the possible influences of the male-male interactions on the lifestyle of recluse spiders. Voucher specimens are deposited at the Coleção de Aranhas do Departamento de Zoologia, UNESP, Campus de Botucatu, UBTU.

METHODS

Test animals and holding conditions.—Forty-four adult male *L. gaucho* were hand-collected from stalk crevices of *Eucalyptus* sp. at the Botanic Garden from IB, UNESP, Botucatu, Brazil (22°59′S, 48°26′W). These animals were maintained in individual glass test tubes (85 mm × 25 mm internal diameter) for about 30 days before the experiments, and fed once a week on insects collected by sweeping. About 3 days before the experiment, the spiders were fed in excess (5 *Musca domestica* per spider) to balance satiation level. The forty-four spiders were used for twenty-two pairwise encounters.

The encounters.—Twenty-two encounters between males were carried out using an intruder-resident paradigm. One spider, designated as the resident, was placed inside the arena (a transparent plastic cage, 110 mm diameter × 70 mm high). This area was about 30–50% bigger than the retreats of *L. gaucho* in the field. One week after this, time enough for the resident to spin its irregular web, the external transparent tube (60 mm long × 40 mm diameter) attached to the arena was disconnected. Another spider, designated as the intruder, was introduced in the tube that was reconnected to the arena. At this point, both the resident and the intruder were allowed to encounter each other.

Spider pairs were selected in order to balance the relative weight between the opponents. Thus, in 11 encounters weight difference was higher than 10% while in the other 11 encounters weight difference was lower than 10%. In the trials with either high or low relative weight, the frequency of residents and intruders with higher weight was also balanced, i.e., residents were heavier in five trials and intruders were heavier in the other six trials. Spiders were weighed with a Mettler H20T balance (160 g; 0.01 mg) one day before experiments. The avg. weight of the specimens was 55.23 ± 15.42 mg (mean ± SD). Each spider was tested only once.

One week before the encounter, one spider of each pair was marked with a nail polish dot on the abdomen to facilitate individual recognition. No toxic effects of this product were observed. Temperature and relative air humidity were kept at approximately 25° C and 70% inside the arenas.

The encounters were tape recorded (VHS system) from above the arenas. Each encounter ended when a "losing" spider was identified (e.g., when either one of the opponents ran away from the rival or abandoned the interaction by moving backwards).

Data analyses.—The behavioral sequences were qualitatively and quantitatively described in a flow diagram (Fig. 1) so that behavioral pathways that ended in aggression and non-aggression could be identified. Aggressive behaviors included lunges or bites (Table 1). Encounters without occurrence of these lunges or bites were defined as non-aggressive encounters. The predominance of these aggressive and non-aggressive encounters was tested using the Chi-square goodness-of-fit test with Yates correction.

RESULTS

The general pattern of encounters between male *L. gaucho* began with the intruders walking into the arena and touching the residents' web (n = 21). In one instance, the resident moved first. After these first movements, in all cases, (n = 22), the intruders vibrated their body appendices; a pattern designated as "VIB" (Table 1 and Fig. 1). Following this, the residents responded by fleeing (n = 9) or interacted using the VIB pattern, i.e., similar to the intruders' behavior (n = 8). The other residents interacted using a postural performance rather than movements, a pattern designated as "POS" (n = 5) (Table 1 and Fig. 1). The duration of the VIB-VIB encounters was of 3–8 min while the duration of the VIB-POS encounters was much longer, 18–37 min. In both types of encounters, the spiders of each pair approached and touched each other with their forelegs (Fig. 1). With the VIB-VIB interaction, when the opponents reached the face-to-face position, they overlapped their forelegs (behavior named "hug" – Table 1) and

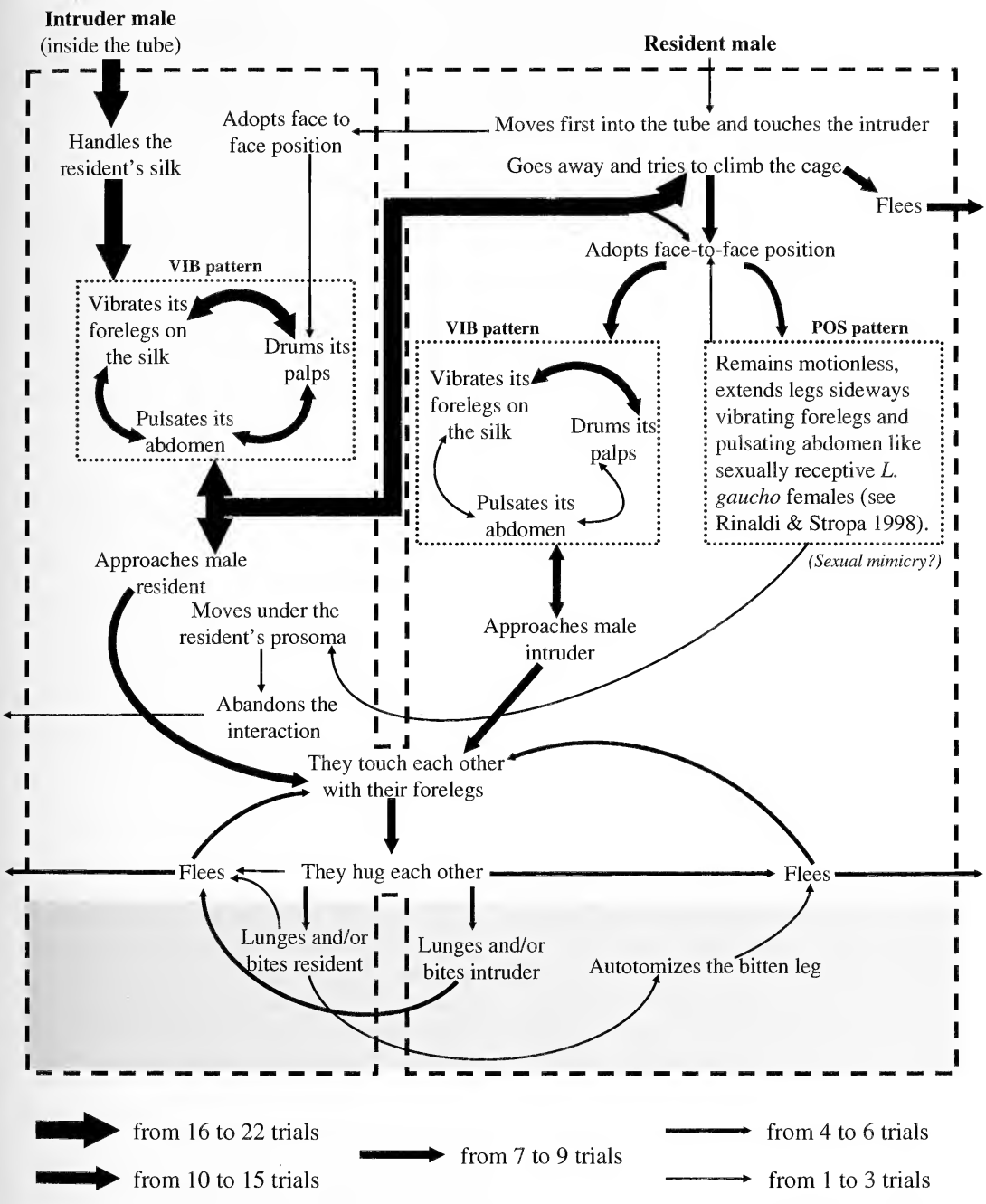

Figure 1.—Flow diagram of the male-male interaction of *L. gaucho* (n = 22). Dashed lines delimit the context. Dotted lines indicate the determined behavioral patterns (movements and/or postures of specific portions of the spider's body). The gray line delimits the period of aggression (area below it). Thickness of arrows indicates the frequency with which the behaviors were observed.

one spider of the pair either fled or lunged at its opponent. On the other hand, when VIB-POS interaction took place, the intruder advanced under the resident's prosoma and then either abandoned the interaction (n = 3), or fled (n = 2). In these last two cases the interaction was longer than 30 min and the residents became aggressive, i.e., they changed from POS into

Table 1.—Behavioral patterns and conspicuous behaviors of the male-male interaction of *L. gaucho*.

Patterns	Behaviors	Description
VIB	Foreleg vibration	Simultaneous vertical movement of the pairs of legs whose tarsi touch the resident's silk.
	Palpal drumming	Alternate vertical palp movements
	Abdominal pulsation 1	Vertical and horizontal abdomen movements
POS	Abdominal pulsation 2	Just vertical movements and slower than the abdominal pulsation 1
	Motionless	Stop walking
	Legs sideways	Extension of all legs sideways
	Hug	Opponents overlap their forelegs (opponents' forelegs touch and beat each other)
	Lunge	One spider jumps abruptly towards its opponent
	Bite	Chelicerae hold a part of the body of a spider and the fangs pierce the cuticle

VIB pattern and immediately the opponents hugged each other and the residents lunged against the intruders.

Non-aggressive encounters were preponderant (77.3%) ($n = 17$: $\chi^2_c = 5.500$, $P < 0.025$). Aggression (occurrence of lunges or bites) took place in just five encounters (22.7%) (Fig. 1), always after the VIB-VIB interaction, even when the residents started their interaction using the POS pattern. In a single aggressive encounter there was physical injury; the injured spider autotomized the bitten leg (Fig. 1).

DISCUSSION

The present study indicates that interactions between male *L. gaucho* are predominantly non-aggressive, at least in the resident-intruder paradigm. When aggression (lunges or bites) took place, it occurred only after the hug. But in this species, the hug does not necessarily trigger aggression since it also occurred in non-aggressive male-male (Fig. 1) and female-female encounters (Stropa & Rinaldi 2001). The hug is possibly used by adult *L. gaucho* spiders to evaluate fighting ability and/or the size of their opponents, allowing for a decision between fleeing or fighting. If this is true; the hug is an aggression-attenuating mechanism since it delays aggression and, as a consequence, improves individual fitness. This situation is predicted in asymmetric animal contests (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Whitehouse 1997).

Two more conspicuous aggression-attenuating mechanisms were found: the fleeing and the POS pattern. Residents fled in 9 of the 22 trials without further interaction with the intruders. This is expected because male spiders may not establish residence in the natural habitat since they move while searching for females (Foelix 1982). Moreover, they are not likely to defend empty territories (e.g., without females or other resources). The present study indicates that intruder males were always interested in interacting with residents displaying the VIB pattern (Fig. 1). However, this interaction was also expected since information about habitat quality can be obtained from other spiders or simply from silk (Hodge & Storfer-Isser 1997; Schuck-Paim & Alonso 2001; Bilde et al. 2002).

An unexpected aggression-attenuating mechanism observed in this study is the POS pattern displayed by five of the 22 residents. In these trials the resident was nearly motionless with the legs stretched sideways, pulsating its abdomen slower than the intruders, and had its prosoma lifted by the intruder advancement. According to Rinaldi & Stropa (1998), when female *L. gaucho* are sexually receptive, they allow males to lift their prosoma to copulate. Males use their own prosoma to lift females, such as the intruders did in the present study. This may not be a simple case of mistaken sexual identity because there were differences in the male-male interaction observed here and the male-female interaction reported by Rinaldi and Stropa (1998). Males interact with females only by palpal drumming, foreleg vibration and abdomen pulsation (Rinaldi & Stropa 1998); e.g., the VIB pattern seen here. Female *L. gaucho* become receptive for mating only by stretching their legs sideways, pulsating their abdomen slowly and keeping themselves nearly motionless (Rinaldi & Stropa 1998); i.e., these

females use only the POS pattern in the sexual interaction. In the present study, male *L. gaucho* used both the VIB and POS patterns in the male-male interaction.

It is possible that the male intruders were courting and trying to copulate with the male residents as if they were receptive females. For spiders, this may be an instance of intraspecific sexual mimicry, which is when an animal gets some advantage over its conspecific opponent by present itself as if it is an individual of the opposite sex. Further investigation is needed to corroborate this hypothesis since only five cases are described in the present study. Sexual mimicry in spiders has been reported only in interspecific interactions such as the bolas spider *Mastophora* sp. attracting prey (Eberhard 1977; Stowe et al. 1987; Yeargan 1994) and *Portia fimbriata* Doleschall 1859 mimicking a male of *Euryattus* sp. (Salticidae) to attack the female hiding in a leaf (Jackson & Wilcox 1990).

The two encounters in which resident males used POS followed by VIB are intriguing and possibly indicate that male *L. gaucho* has some behavioral plasticity. In both cases, the contest escalated to aggressive behaviors after the resident displayed VIB, and the resident won the contest. According to Horel et al. (1996), behavioral plasticity is a pre-adaptation for social life in spiders since it amplifies the intraspecific tolerance. This hypothesis may explain male pairs of this species sharing retreats in the field during the day (Stropa 2004).

In conclusion, the intraspecific interaction of male *L. gaucho* in the resident-intruder paradigm is usually non-aggressive. This profile is a result of the three aggression-attenuating mechanisms identified: the hug, the fleeing and the POS pattern. These mechanisms may facilitate group living. Recluse spiders have been classified as solitary and territorial (Bücherl 1961; Weens & Whitcomb 1975; Japyassú et al. 2003), but according to several reports they also live in conspecific aggregations and infest manmade environments (Bücherl 1961; Levi & Spielman 1964; Howner & Stewart 1967; Waldron et al. 1975; Fischer & Vasconcellos-Neto 2005; Marques-da-Silva et al. 2006). The investigation of the causes of these aggregations might reveal the main factors modulating the lifestyle of recluse spiders and might elucidate mechanisms that minimize infestation in manmade environments where *Loxosceles* can become a public health problem. However, interaction is only one factor to be considered and it is certainly linked to other variables such as resource availability and habitat architecture.

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HUNTING PREY WITH DIFFERENT ESCAPE POTENTIALS—ALTERNATIVE PREDATORY TACTICS IN A DUNE DWELLING SALTICID

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ABSTRACT. Generalist predators hunt a wide range of prey that possess various characteristics affecting the predators' hunting success (e.g., size, ability to detect the threat and defend against it, potential for escape). Therefore, it can be expected that the predator should flexibly react to different prey characteristics, hunting them in prey-specific ways. For a stalking predator a crucial prey feature is its ability to escape. In this study, the alternative prey-catching tactics of a dune-dwelling salticid *Yllenus arenarius* Menge 1868 were analyzed. Four naturally eaten prey taxa, two with a high ability to escape (Homoptera, Orthoptera) and two with a low ability to escape (Thysanoptera, larvae of Lepidoptera), were used. Numerous differences found between the tactics indicate that *Y. arenarius* can not only distinguish between different types of prey, but can also employ specific tactics to catch them. The tactics belong to a conditional strategy and are manifested in alternative: a) direction of approach, b) speed of approach, and c) other prey specific behaviors.

Keywords: Predatory behavior, conditional strategy, spider, Araneae, Salticidae, *Yllenus*

There are numerous examples of alternative phenotypes expressed through animal morphology, life history, and behavior. They are most commonly reported in the field of reproductive biology (reviewed in Gross 1996) and studies of resource-based polymorphisms (reviewed in Skúlason & Smith 1995). The examples are readily interpreted as alternative tactics within a conditional strategy—a concept proposed by Gross (1996). In their theory (Gross & Repka 1998) it is postulated that: a) the tactics involve a choice or decision by the individual; b) the decision is made relative to some aspect of the individual's state or status; c) all individuals in the population have the same genetically-based strategy and the genes for expressing the tactics; d) the average fitnesses of the tactics are unequal; and e) the chosen tactic results in higher fitness for the individual.

The examples of conditional strategies expressed through behavior focus our attention on both the perceptual ability to distinguish between alternative options and the flexibility of animal behavior. Therefore the animals possessing certain limitations to their neural system are of special interest (Jackson 1992; Wilcox & Jackson 1998; Harland & Jackson 2004). Among invertebrates, conditional strategies were found in the behavior of spiders and shown to be common in salticids (Jackson 1992; Edwards & Jackson 1993, 1994; Bear & Hasson 1997).

Conditional strategies are present in both alternative mating tactics and predatory behavior of jumping spiders (Jackson 1992; Edwards & Jackson 1993, 1994; Bear & Hasson 1997). The studies of mating behavior in numerous salticids revealed that the type of male courtship depends on the female's maturity and location (inside vs. outside the nest) (Jackson 1977). Predatory tactics of jumping spiders, conditioned by the prey type and location, provided even more fascinating examples of an extraordinary versatility in these arthropods (Jackson 1992; Jackson & Pollard 1996; Wilcox & Jackson 1998).

Jumping spiders are especially good models to study conditional predatory strategy. This is due to their complex behavior (Richman & Jackson 1992; Jackson & Pollard 1996) and particularly well developed sense of vision (Land 1969a, b; Williams & McIntyre 1980), which enables discernment between various prey characteristics (Harland et al. 1999; Harland & Jackson 2000, 2001, 2002). As a result, the predators can choose a tactic out of an available repertoire on the basis of visual discrimination only.

In many ways, salticid eyes are exceptional among invertebrates. Taken together, the eyes

give a visual field of almost 360° around the cephalothorax (Land 1985). Three pairs of so called "secondary eyes" serve merely as movement detectors, whereas one pair of frontally positioned "principal eyes" has, in fact, much more advanced optical performance than complex insect eyes (Uetz & Stratton 1983; Land 1997; Harland & Jackson 2000) allowing color vision (Blest et al. 1981) and precise shape recognition (reviewed in Forster 1985). The actual distance from which some species can distinguish a prey from a conspecific is equivalent to 47 spider body lengths (Harland et al. 1999). Moreover the spatial acuity of the principal eyes exceeds the spatial acuity of the best seeing insects by tenfold (Harland & Jackson 2004).

The hunting success of a stalking predator is the result of numerous decisions made during the approach stage and capture and depends primarily on the prey's ability to perceive the predator and escape. As summarized by Bear & Hasson (1997), who studied the approaching speed and the striking distance of *Plexippus paykulli* (Audouin 1826), a stalking predator may fail for at least four reasons: if the prey perceives the predator before the attack, releases and escapes after the strike, or spontaneously moves away in the course of its natural activity, even without perceiving the danger. Finally a competitor or the hunter's own predator may influence the outcome of the encounter (before or even after the attack). The analysis of the potential risks reveals numerous trade-offs between contradictory decisions (e.g., slow approach decreases the risk of being noticed but increases the risk of the prey's spontaneous departure). Therefore, each of the alternative behaviors is associated with different pay-offs. To what extent spiders can assess some of the trade-offs and whether they flexibly react in different situations is extremely interesting but poorly represented in the studies (Bear & Hasson 1997). The purpose of the current research is the analysis of prey-specific alternative behaviors in order to assess the extent of the behavioral predatory flexibility of a salticid and to characterize trade-offs that may influence the choice of a tactic.

Yllenus arenarius Menge 1868 is a medium-sized jumping spider with an adult body length of about 7 mm, occurring in Central and Eastern Europe (Logunov & Marusik 2003). This cryptically colored spider dwells in sparsely vegetated dunes, where it occupies the areas of bare sand between the grass. An extremely important adaptation for survival in this habitat, which lacks hiding places, is burrowing behavior and the ability to construct sub-sand nests. The nests are built for various purposes (molting, egg-laying, and hibernating) and provide shelter against night-active predators, strong wind and periods of inclement weather (Bartos 2002b). *Yllenus arenarius* is a polyphagous, sit-and-wait predator feeding on a wide range of invertebrates that inhabit open sand or are blown by the wind onto the dune surface from neighboring habitats (Bartos 2004).

METHODS

Prey.—On the basis of a diet analysis carried out before the experiments (Bartos 2004) four taxa of common, natural prey were chosen, markedly different according to their ability to escape. These were: Homoptera, Orthoptera, Thysanoptera, and larvae of Lepidoptera (Table 1). Two of them (Homoptera and Orthoptera) possess wings and/or jumping legs, which enable effective escape and were therefore regarded as prey of high escape risk. Thrips and caterpillars are unable to move quickly and were considered prey of low escape risk.

The prey items were collected in the field by sweep-netting dune grass on the day of the experiment or the day before. They were brought to the lab and kept individually. Each prey item was given to the spider of approximately similar size. In order to reduce mortality of the prey, insects were stored in a refrigerator (5° C) and taken out 15 min before the experiment started.

Predators.—Predators and prey were collected from a dune in Central Poland (Kwilno, 51°59′ N, 19°30′ E). Spiders were collected on the day of the experiment or the day before in order to reduce the influences of rearing conditions on the spider's behavior. Such procedure did not alter the spiders' natural behavior, which may be easily affected by laboratory rearing (Carducci & Jakob 2000; Bartos unpubl. data). This method, however, did not allow us to control for the predator's hunger level. The possible influence of different hunger levels was balanced by random selection of the spider and random choice of one of four prey types. Before the experiments spiders were kept individually in glass containers (height, 10 cm; width, 10 cm) with a layer of dune sand

Table 1.—Prey taxa used in the experiments.

Prey species	Order and family	Ability to escape	Body length (mm)
Psammotettix sp.	Homoptera, Cicadellidae	High	4–5
Omocestus haemorrhoidalis	Orthoptera, Acrididae	High	4–6
Chorthippus brunneus	Orthoptera, Acrididae	High	4–6
Cryptothrips nigripes	Thysanoptera, Phlaeothripidae	Low	2
Thrips trehernei	Thysanoptera, Thripidae	Low	1
Chirothrips manicatus	Thysanoptera, Thripidae	Low	1
Pyralis farinalis	Lepidoptera, Pyralidae (larvae)	Low	4–8
Autographa gamma	Lepidoptera, Noctuidae (larvae)	Low	4–8

on the bottom. Adult individuals of *Y. arenarius* are characterized by strong sexual dimorphism expressed in color and pattern. The intersexual differences appear after the final molt and may influence the hunting behavior of one sex (Givens 1978; Bartos unpubl. data), therefore only juveniles (body length ca. 4.5 mm) and females (body length ca. 6 mm) were used in the experiments. Approximately the same number of individuals from each age group was used. Each spider was chosen randomly and used only once in the whole set of tests. The total number of spiders tested was 981, but only in ca. 25% were hunting sequences observed. The experiments in which no hunting behavior was present (e.g., because the spider ignored the prey or the prey escaped before it was approached) were not included in the analysis. The number of experiments in which the spider hunted the prey is given as *n*.

Experimental procedure.—Experiments were carried out within a white cardboard arena (height, 15 cm; diameter, 20 cm) with a 1 cm-thick sand layer on the bottom. All the experiments were conducted between 09:00 and 16:00 hours (laboratory light regime, 12L:12D, lights coming on at 08:00 hours). Lighting was from a 100W PILA incandescent lamp bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena. Spiders were placed within the arena and, after 1 min, a prey item was introduced about 8 cm from the spider. The prey was dropped approximately 30° to the left or right from the main eye's optical axis to allow the experimenter to record the moment when the predator perceived the prey. The prey was left with the spider for 15 min. The hunting behavior was recorded with a camera placed above the arena.

Data analysis.—Movies with hunting sequences were analyzed, the behaviors observed, and the hunting success was recorded. The complete sequences of hunting, namely those that started with the first dynamic behavior (run), and that ended with subduing the prey were used to draw flow diagrams (Figs. 1–4). If there were multiple attacks of a spider on the same prey, only the first hunting sequence was included. The percentage of individuals that expressed certain behaviors is indicated by the width of the line that leads to the behavior and by the number above the line. The numbers in some paths do not add up to 100% due to rounding.

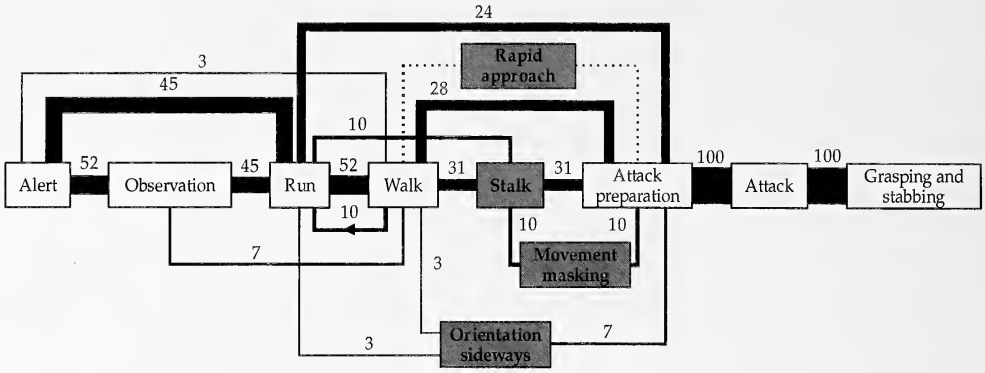
Since the modes of hunting prey with both high and low ability to escape demonstrate many similarities, the complete series of behavioral units typical for hunting each kind of prey is given only in the first description below. In the account of the hunting sequence for prey that cannot escape, only a description of the prey-specific behaviors is presented. Names of other already reported components of salticid behavior are taken from a classic paper by Forster (1977).

All statistical procedures followed those described by Zar (1984). To test the differences in frequency of behavior in hunting different prey types, the Pearson's chi-squared test was used.

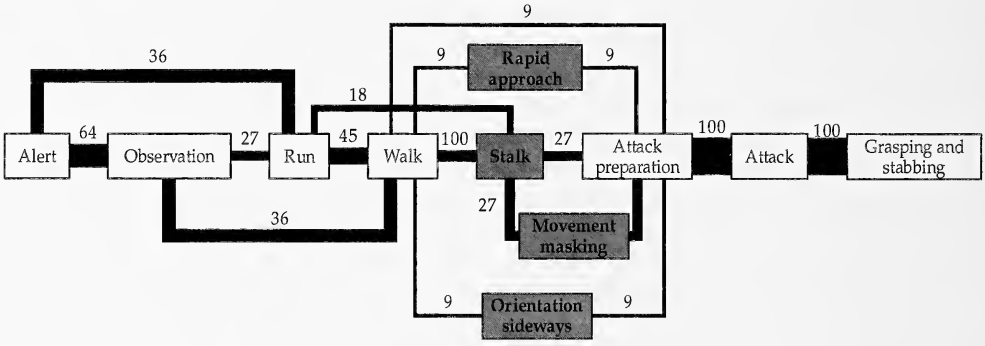
RESULTS

The pattern of hunting prey with different escape potentials.—When hunting prey with a high ability to escape, irrespective of the prey taxon, the first easily discernible element was "alert" characterized by movement of the cephalothorax or of the whole body, which resulted in directing the main eyes towards the prey (Figs. 1–4). Spiders observed the prey for

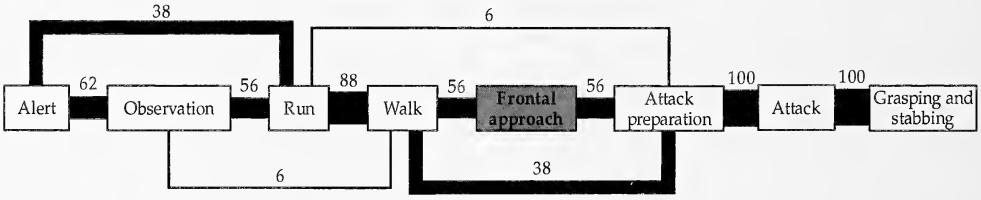
1) Homoptera



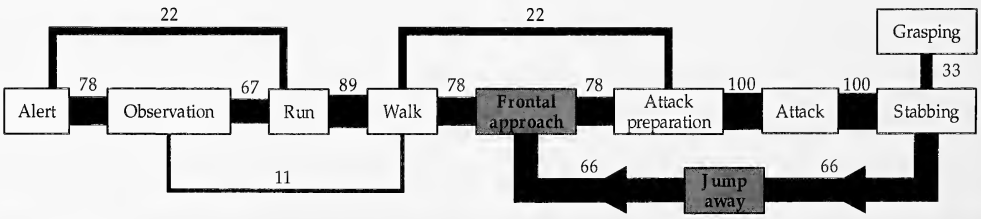
2) Orthoptera



3) Thysanoptera



4) larvae of Lepidoptera



Figures 1–4.—Flow diagrams of *Y. arenarius* hunting four prey taxa. 1. Homoptera (n = 29); 2. Orthoptera (n = 11); 3. Thysanoptera (n = 16); 4. larvae of Lepidoptera (n = 9). Transition frequencies are indicated by the per cent numbers and by an appropriate line width. Dotted line symbolizes the behavior that was not observed in the complete hunting sequence but was commonly recorded in incomplete sequences. Grey boxes indicate prey-specific behaviors. The sequence should be read from left to right unless indicated by an arrow.

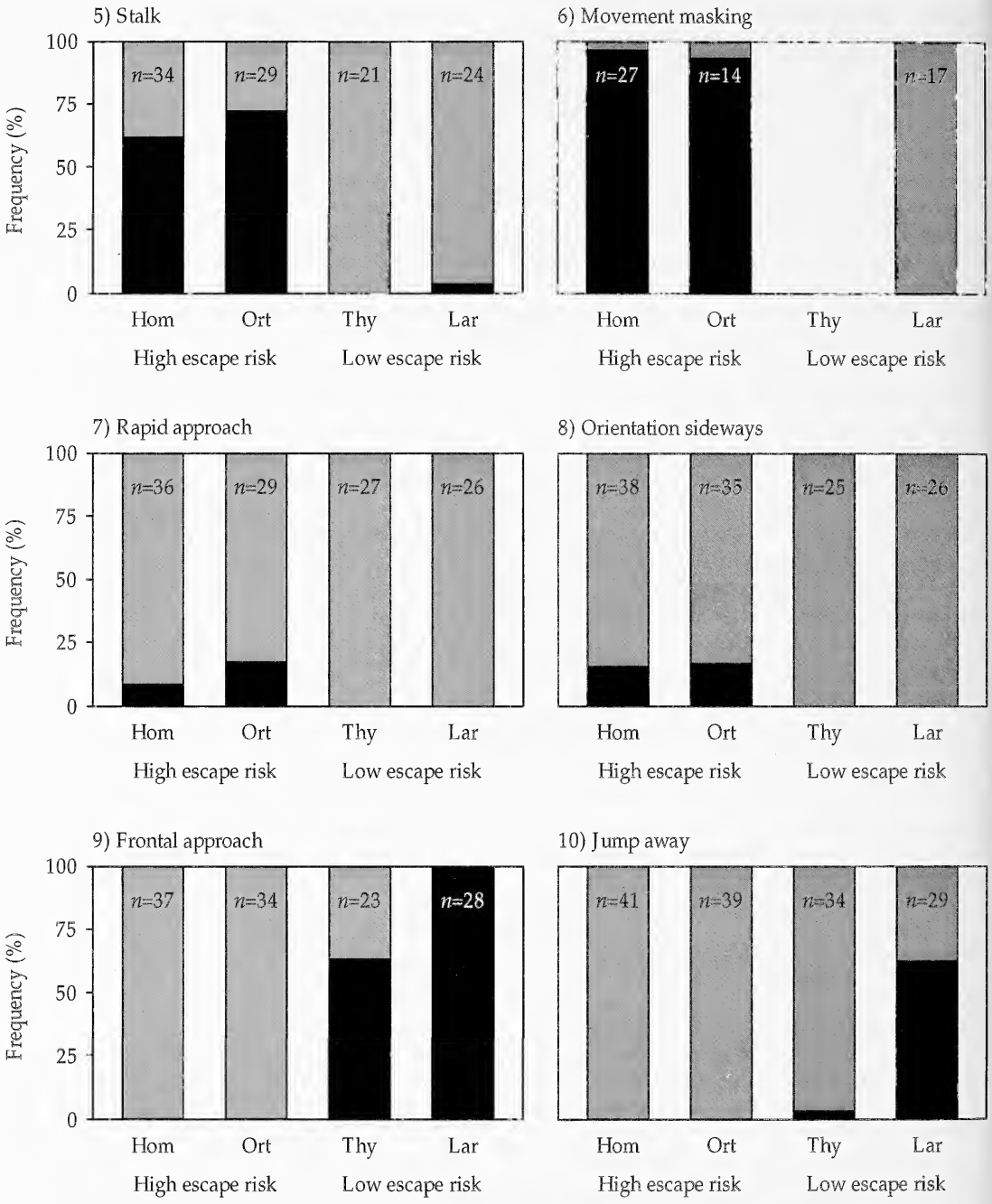
usually less than a minute and ran towards it in bursts. The closer spiders got to the target, the slower was their movement. They decelerated to a walk and subsequently stalked prey with a slow, "cat-like" motion. Another slow type of approach called "movement masking" was observed when the prey moved and froze alternately and, following the prey movements, the spider approached only when the prey changed its position; e.g., began cleaning its body or slowly moving. The spider froze or decelerated when the prey stopped moving. An alternative mode of approach using a long jump or quick run in the direction of prey was called "rapid approach" (Figs. 1, 2). Spiders using this tactic landed or stopped running very close to the target and attacked after only a short sequence of preparation for the attack. In a few cases the predators did not approach directly, but orientated sideways going round the prey with a rapid, crab-like movement (Figs. 1, 2). During the activity, spiders always orientated themselves towards the prey, but never approached frontally.

Directly before the attack, a series of four characteristic preparatory movements was observed. Spiders a) lowered their bodies spreading legs sideways, b) attached dragline to the sand surface, c) rapidly pushed sand with the fourth pair of legs, and finally d) raised the first and sometimes also the second pairs of legs in the direction of the prey. The attack occurred in all cases of hunting Homoptera and Orthoptera by means of a jump and took place soon after the frontal leg raising. After landing on the prey's back, the insect was embraced with legs and finally pierced with fangs. In a few cases, prey managed to escape or was released after the first direct contact and the predator usually withdrew. However, the prey was neither observed by the spider after such abandonment nor was the attack repeated.

The sequence of events in hunting thrips and caterpillars was shorter and less complex, but most units described in hunting Homoptera and Orthoptera were also present here (Figs. 3, 4). The specific behaviors concerned the direction of approach or prey handling after attack. Spiders approached the anterior part of the prey's body rather than the abdomen. Such behavior, defined as "frontal approach," was characterized by circling the prey (if the prey was not facing the spider before approach). As a consequence of this tactic the spider found itself in front of the moving prey, either waiting on its supposed track or actively approaching the prey. After the attack preparation, spiders jumped on the prey or walked and stabbed it with most bite punctures found on the dorsal side of the second and the third segments of the thorax. Caterpillars were most frequently released after venom injection and, after jumping away from the caterpillar, the predator stayed close, constantly observing the wriggling prey. After a period of time, the attacks were repeated and up to eight strikes were observed before the prey was finally subdued.

Behavioral prey-specificity.—Prey-specific behaviors were observed when the predator was in the proximity of the target. While moving towards Homoptera and Orthoptera, the predator decelerated and, when close, stalked them. Such behavior was almost never observed in approaching thrips and caterpillars (Fig. 5) ($\chi^2 = 46.32$, $df = 3$, $P < 0.001$). Another behavior specific for hunting more mobile prey was "movement masking," which was never observed in approaching caterpillars (Fig. 6) ($\chi^2 = 49.41$, $df = 2$, $P < 0.001$). "Movement masking" could not be recorded when hunting thrips since it requires the prey to alternately slow down and then speed up. This does not occur in thysanopteran movement, which is generally uniform in speed and with only sporadic pauses when on the open sand. Two other behaviors specific for hunting Homoptera and Orthoptera were "rapid approach" ($\chi^2 = 10.81$, $df = 3$, $P < 0.05$) and "orientation sideways" ($\chi^2 = 9.32$, $df = 3$, $P < 0.05$). Neither of the behaviors was observed in cases of hunting Thysanoptera and larvae of Lepidoptera (Figs. 7, 8).

Interestingly, the prey of high and low escape risk was attacked from different directions. While thrips and caterpillars were circled and approached from their front side, no such definite attack direction was preferred in hunting Homoptera and Orthoptera ($\chi^2 = 97.74$, $df = 3$, $P < 0.001$) (Fig. 9). The mode of handling prey directly after attack also differed between the groups ($\chi^2 = 75.32$, $df = 3$, $P < 0.001$). Homoptera and Orthoptera were never released after venom injection (Fig. 10). In only one out of 34 episodes of hunting thrips was the prey released and, after a short time, attacked again and subdued. Repeated attacks with venom injection were followed by release of the prey. Hunting prey of low and high



Figures 5–10.—Frequency of six prey-specific behaviors in hunting Homoptera (Hom), Orthoptera (Ort), Thysanoptera (Thy) and larvae of Lepidoptera (Lar) by *Y. arenarius*. The behaviors are: 5. Stalk; 6. Movement masking; 7. Rapid approach; 8. Orientation sideways; 9. Frontal approach; and 10. Jump away.

escape risk differed also according to the hunting success ($\chi^2 = 7.56$, $df = 1$, $P < 0.01$). All cases of catching thrips ($n = 34$) and caterpillars ($n = 29$) were successful in comparison to 95% of homopterans ($n = 41$) and 82% of orthopterans ($n = 39$).

DISCUSSION

The pattern of hunting prey with different escape potentials.—The hunting behavior observed in *Y. arenarius* was similar to those of other non-specialized salticids approaching comparable prey (Forster 1977, 1982; Edwards

& Jackson 1993, 1994; Bear & Hasson 1997). Three phases: orientation, pursuit, and capture, reported by Forster (1977) were easily discernible in hunting all four prey taxa. Although the general pattern of approach was similar for hunting prey of both high and low ability to escape, the differences in hunting them were clearly discernible only when the predator got nearer to its prey, namely at the stage of pursuit and capture (Figs. 1–4). Obviously, once the predator was closer to the prey, the prey could more easily perceive the predator and escape, if able to do so. At the beginning of the hunting session, both prey types were approached in a similar way from a relatively long distance away: quickly and without any apparent measures taken to reduce the predator's visibility to the prey (Figs. 1–4). Such distance-dependent behavior is typical for many predators that stalk their prey (Curio 1976).

Alternative tactics.—Numerous differences found between the tactics of hunting four prey taxa indicate that *Y. arenarius* can both distinguish between different types of prey and employ a specific mode of hunting to catch them. The choice of a tactic takes place after a period of observation. According to the definition of the conditional strategy summarized in the introduction (Gross & Repka 1998), the tactics observed in *Y. arenarius* may be defined as a part of conditional strategy in which the decisions concerning the mode of approach seem to depend primarily on both the prey's ability to escape and the predator's visibility to the prey. The behavior that increases hunting success must obviously result in higher fitness to the predator. The alternative tactics were expressed in four aspects of hunting: direction and speed of approach, specific behaviors and finally jumping distance, which was discussed elsewhere (Bartos 2002a).

Direction of approach: Both prey of low and high risk of escape were approached differently. No specific path was preferred when hunting Homoptera and Orthoptera. They were approached directly irrespective of their position. Such a path might increase hunting success not only because it is the fastest way of reaching the target, but also because it reduces the risk of being perceived by the prey if it was circled. These advantages of direct approach are reflected in the widespread occurrence of the tactic among salticids (Freed 1984; Edwards & Jackson 1993, 1994; Bear & Hasson 1997).

"Frontal approach," the direction specific for prey that had limited ability to escape, was recognizable shortly after the spider had moved in the direction of the prey. This suggests both quick prey recognition and flexible choice of hunting tactic. Running around prey that cannot escape may be advantageous for several reasons. First, the predator attacking frontally grasps the prey by the dorsal side of the thorax and head, thus neutralizing the prey's jaws, and defensive fluids commonly spit out of the prey's mouth (Edwards & Jackson 1993; Salazar & Whitman 2001; Bartos unpubl.). A wriggling caterpillar is also less effective at throwing the spider away and hitting it against the ground if the spider does not jump away. Furthermore, the attack from the front side enables firm prey grasping (proportional from both sides) and fang piercing which, in consequence, allows precise venom injection. Logically, the faster the prey is paralyzed, the lower risk of injury or perception of the prey (and the spider) by other predators.

It is interesting that prior to the strike on caterpillars and thrips the spiders kept a close and fairly constant distance to the prey's head, but avoided premature contact with the prey's body, withdrawing when the prey approached too close. Such behavior was also reported by Edwards & Jackson (1993), which suggests that early detection may also play a role in the case of prey with low ability to escape, possibly diminishing the predator's chances to strike and grasp the prey precisely.

Speed of approach: Although in my research the predator's velocity was not directly measured, it is quite clear, analyzing certain behaviors preceding the attack, that prey with high risk of escape is approached slowly ("stalk" and "movement masking") while prey with low risk of escape is approached without such preventative measures. This kind of a relationship between the speed of approach and distance to prey has been neatly shown by Bear & Hasson (1997) in their study of *P. paykulli.*

Prey-specific behaviors: Some prey-specific behaviors observed in the course of prey capture in *Y. arenarius* (e.g., "stalk," "orientation sideways," "frontal approach") are also reported in the studies of other salticids (Forster 1977, 1982; Edwards & Jackson 1993, 1994) and seem to be universal elements of the hunting strategy in jumping spiders. However, during the research some prey-

specific behaviors (e.g., "movement masking," "rapid approach," "sand firming before the jump," "jump away") were not reported elsewhere and therefore they are possibly unique for *Y. arenarius*. Some of the behaviors constitute essential components of the alternative tactics and therefore are discussed in detail.

"Movement masking" seems to be a very effective tactic against more mobile prey. It is in many aspects similar to "opportunistic smokescreen behavior" reported for *Portia* approaching prey on alien webs (Wilcox et al. 1996; Jackson et al. 2002) and even more to "cryptic stalk" observed only when *Portia* approaches other salticids (Harland & Jackson 2001). In all cases the predators exploit situations in which the prey's ability to detect the spider is impaired. Web-invaders approach host spiders using a smoke-screen when the host webs are subjected to vibrations masking the predator's footsteps. While approaching egg sacs or insects ensnared in the web, salticid web-invaders do not perform the smoke-screen behavior (Wilcox et al. 1996; Cerveira et al. 2003). *Portia* stalking prey cryptically holds its palps back beside the chelicerae and uses a slow, choppy gait, freezing when faced by its salticid prey. Harland & Jackson (2001) observed that most salticids fail to recognize a cryptically stalking *Portia* as predator. Similarly *Y. arenarius* approaches cryptically when the prey moves (changing position, cleaning legs or antennae), which decreases its ability to perceive a moving predator. Such behavior is observed, however, only when the prey is able to escape. Therefore, although "opportunistic smokescreen behavior" and "cryptic stalk" have been only recorded for web-invading araneophagic spartaeines (Wilcox et al. 1996; Cerveira et al. 2003), in a broad sense the general pattern of behavior may be widespread among other salticids.

Some spiders that hunted the prey with high ability to escape did not stalk but approached their prey rapidly. This alternative way of approach, which obviously increases the risk of a prey's escape, may also have some advantages. Although the conditions influencing the choice of the tactic cannot be precisely determined at this stage of analysis, one of the possible factors that may play a role seems to be the risk of the prey's spontaneous departure (Bear & Hasson 1997). Both Homoptera and Orthoptera unpredictably move from one place to another, therefore the high risk of being noticed by the prey may be balanced by the advantage of quick and sudden attack.

"Orientation sideways" was another intriguing behavior observed in close proximity to the prey. Similarly to rapid approach, orientation sideways also deviated from the general pattern of approach to the prey with high ability to escape, which may be summarized as: "the closer to the prey, the less conspicuous the predator's behavior." Such pattern may also be observed in the gradual changes of approaching speed in *P. paykulli* (Bear & Hasson 1997) and results from the increasing ability of the prey to detect the predator as it comes nearer. The possible function of the behavior seems to primarily be identification. Sideways movements enable prey perception from different angles and as a result give a three-dimensional representation of the observed object. Such behavior may also improve estimation of distance to the prey.

Orientation sideways must significantly increase the risk of being detected, but there are, however, circumstances that may counterbalance the risky tactic. The most likely factors seem to be those connected with potential threat that a prey animal may pose to the predator. As a polyphagous predator *Y. arenarius* also hunts prey possessing powerful jaws and stings (Bartos 2004). Some of the prey animals (e.g., solitary bees, ants) resemble those which were frequently observed to parasitize or feed on the spider (e.g., pompilid wasps, other ant species or castes) (Bartos unpubl.). Therefore, precise prey identification and determination of the area of grasping and venom injection are extremely important tasks.

"Jump away," the behavior specific for *Y. arenarius* hunting caterpillars, has not been described in other studies on salticids hunting insect larvae (Edwards & Jackson 1993, 1994; Bear & Hasson 1997), but similar behavior was reported for several species of *Aelurillus* hunting wingless ants (Li et al. 1999). "Jump away" seems to be a good adaptation to minimize the risk of interference with the spider's own predators (Bear & Hasson 1997) and reduce the possibility of getting injured by the prey. On the surface of bare sand dunes, any movement may attract predators. The most serious threat constitutes tiger beetles, robber-flies, and ants, or some less numerous vertebrates such as birds or lizards (Bartos unpubl.). The best strategy to

avoid the movement-sensitive predators would be to stay motionless and keep away from any object that attracts a predator's attention (Pearson 1988). A cryptically colored spider that stealthily waits until the prey is paralyzed obviously reduces both the risk of being detected by its own predators and the risk of getting injured by the prey than the one that tries to overpower a writhing caterpillar.

The prey with high risk of escape was never released after being captured. This is presumably because the period from venom injection to prey immobilization would be long enough to enable efficient escape or blowing the prey away by wind. My numerous observations of orthopterans and homopterans jumping for several minutes with a spider on their backs before they became paralyzed, support this assumption. Similarly, thrips, which are fairly delicate but winged prey with markedly limited escape potential, were not released after attack. They were, however, usually kept hidden between the legs and under the predator's body, therefore their visibility and the risk of injury to the spider was possibly limited.

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REVIEW ARTICLE

BIRD PREDATION ON SPIDERS: ECOLOGICAL MECHANISMS AND EVOLUTIONARY CONSEQUENCES

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ABSTRACT. Birds are common predators of arthropods in many ecosystems but their impact on spiders has not been assessed. Therefore, the experimental evidence for bird predation effects on spider populations was examined. In particular, the present review focuses on the questions: what are the ecological mechanisms and what are the evolutionary consequences? Data from 17 field experiments, mainly in forest ecosystems, showed that spider communities were often significantly affected by bird predation. Comparisons of experimental effects were based on the ratio of mean density on experimentally enclosed vegetation and on controls. In 27 tests, a significant effect was detected (mean ratio 3.03) but in 9 tests the effect was non-significant (mean ratio 1.03). Furthermore, field experimental studies on bird predation effects on certain spider species or certain genera were reviewed. In three investigations, significant predation effects were found on agelenid, linyphiid and theridiid spiders but there were no significant effects on lycosids. Selective bird predation on large individuals has been shown in studies on spider communities and single species. Data on bird predation effects on species richness were lacking although impact on large species was expected to be important. Three field experiments showed that different spider families may experience differences in bird predation pressure. An aviary experiment showed that frequently moving spiders had a higher risk of predation than sedentary individuals, but the evidence from field experiments supporting the hypothesis of high predation pressure on moving spiders was limited. This included sex-specific differences in size and movement, although at least one experiment showed that males had higher winter mortality than females. One experiment showed that bird predation can affect anti-predator behavior. In conclusion, the present evidence showed that bird predation on spiders in several contrasting forest ecosystems is strong. However, there are many hypotheses regarding bird predation on spider populations that should be examined in future field experiments.

Keywords: Avian predation, field experiments, natural selection, spider community

Birds in terrestrial habitats consume insects and other arthropods in large quantities. This fact has recently led a number of authors to emphasize the importance of bird predation as part of the "ecological services" that human societies rely upon (e.g., Sekercioglu et al. 2004; Fayt et al. 2005; Sekercioglu 2006). Many studies have focused on the economic importance because of the large values that can be gained by reduction of insect herbivore populations in agricultural areas or managed forests (Takekawa & Garton 1984; Mols & Visser 2002). However, insectivorous birds are often generalists and may feed on many trophic levels. This means that birds are not only eating herbivores that are damaging human food or other resources, but also include in their diet arthropods (e.g., spiders) that otherwise compete with birds for insect prey.

Arachnologists have long acknowledged birds as a potential threat against spider populations but they have had different opinions about their importance. In the first edition of "Biology of Spiders" Foelix (1982) stated that "The influence of birds as a factor controlling spider populations is generally overestimated." He argued that spiders often hide, sit motionless, are cryptic, or are active during the night and, therefore, spiders would be poorly perceived by birds. Moreover, he said that adult birds rarely eat spiders but certain species may feed spiders to their young. There were no references to support these claims. In the second edition, Foelix (1996) added that "spiders are a major prey for many birds during winter" and referred to the works by Askenmo et al. (1977) and Hogstad (1984). Thus, results from experimental studies have gradually been

accepted in textbooks but still much of the data referred to are from old, mainly descriptive studies. Wise (1993) in his book on spider ecology discussed birds as important natural enemies of spiders and referred to several experimental works. He concluded "birds take substantial numbers of overwintering spiders from spruce branches, and birds have been implicated as important predators upon large orb weavers in tropical forests." Thus, in this book birds are rated among the most prominent predators on spiders. However, in more recent papers, authors have questioned whether birds really are important as mortality agents (e.g., Blackledge et al. 2003).

The present review is not intended to be an exhaustive evaluation of all papers discussing the importance of birds as predators on spiders or their egg-sacs. There have been many conclusions about the effects of bird predation on spider populations based on rather poor data or interpretations that go beyond the data at hand. Instead, the focus in the present paper will be on the experimental evidence for the impact of birds on spiders in natural populations. Experiments in field ecology have become increasingly popular as a way to examine hypotheses about predation in different habitats (Hairston 1989). Many of the conclusions in Wise's (1993) book on spider ecology were based on experimental evidence. The experimental approach has certain advantages. Experiments provide good insights into cause and effect and are a means to test hypotheses. This approach may also help to disentangle complex interactions in natural habitats. It was in the 1970s that field experiments of bird predation on spider populations became well established in the ecological literature (e.g., Askenmo et al. 1977; Holmes et al. 1979). These pioneering experiments and their successors will be the focus of the present review.

Two questions of importance will be highlighted: what are the ecological mechanisms of bird predation on spiders, and what are the evolutionary consequences? In a previous review of bird predation on arthropods, Holmes (1990) emphasized these two functions of bird predation. First, I will present some work on birds' diets. Second, experimental studies on bird predation effects on spider assemblages will be scrutinized. Third, investigations of bird predation on single species are reviewed. Fourth, the importance of birds as selective agents on spider populations is summarized. Finally, bird predation on spiders is evaluated in an ecological and evolutionary context and this also leads to new hypotheses.

SPIDERS AS BIRD PREY

Bristowe (1941) referred to several field observations of birds eating spiders, especially in investigations on the effect of birds on pests, in the early 20th century. However, the importance of spiders as prey of birds has mainly been supported by analyses of stomach contents and fecal samples. In his review of spider enemies, Bristowe (1941) evaluated the importance of bird predation as a mortality agent of spiders mainly by using data from stomach analyses. The stomach data were used to estimate average numbers of spiders eaten by various bird species suggesting, e.g., that a blackbird would eat 106 spiders per year. In further calculations, various assumptions and rough estimates about population sizes of birds and spiders led to the conclusion that birds in England and Wales did not pose a serious "threat" to spider populations (Bristowe 1941). In terms of population dynamics this means that Bristowe suggested that birds did not control (regulate) spider populations.

Stomach analysis has often been used to identify the number of individuals of various prey items. For instance, in a quantitative examination of prey of goldcrests (*Regulus regulus*) in winter, Hogstad (1984) suggested that, on average, 60% of the individual prey were spiders. In mid-winter (January and February) the percentage increased to about 80%. On the other hand, spiders can be quite rare in other birds' diets. In an analysis of the stomachs of the meadowlark (*Sturnella magna argutulla*) in Florida, Genung & Green (1974) found a few remains of lycosids in 12.7% of 63 birds examined.

Another possible approach was to examine fecal samples. The feces were easier to sample and the sample size could often increase considerably in comparison to stomach samples. It was also convenient because birds were not harmed by sampling. For instance, in a study of the threatened California gnatcatcher (*Polioptila c. californica*), fecal samples showed that the adult gnatcatchers selected more and larger prey, including spiders, to feed their chicks than adult birds ate themselves (Burger et al. 1999). However, there was constantly a

risk that estimations of prey numbers would be biased. In a study of the diets of the willow tit (*Parus montanus*) and crested tit (*P. cristatus*), Jansson (1982) showed that numbers of spiders and beetles were overestimated in fecal samples in comparison with estimates of prey brought to the nest by using color photographs from cameras at the nest entrance.

Both stomach analysis and fecal samples have a number of important limitations when assessing the importance of bird predation. First, the digestion of prey makes it difficult to correctly assess the numbers of various prey taxa. It is true that many arthropods have distinctive sclerotized body parts but still it could be hard to provide counts of individuals based on different numbers of cheliceral fangs, tarsal claws, leg parts, etc. Second, biased data will lead to incorrect estimates if it is magnified several times. Samples including a few bird individuals will not be sufficient for an unbiased estimate of the predation pressure on the arthropod prey. Third, the relevance of bird predation on spider populations is dependent on local abundance and this is usually unknown in studies based on ingested food. If the population size of the spiders is rather small but increasing, then relatively moderate predation pressure can cause a significant decline of spiders locally. On the other hand, even high predation pressure by birds would not influence an extremely large population to any significant extent. These types of interactions between birds and their arthropod prey have been observed in several study systems in forests (e.g., Crawford & Jennings 1989; Holmes 1990). Different spider populations probably show a similar response to varying bird predation pressures. In order to evaluate the importance of bird predation on local spider populations, some estimate of the effect of the predation must be made, preferably by comparing data on spiders exposed to birds vs. spiders protected from bird predation.

BIRD PREDATION ON SPIDER ASSEMBLAGES / COMMUNITIES

Studies on spider assemblages, or communities, offer good opportunities to evaluate the impact of bird predation. The advantages of such studies are that it is usually easier to study the effects of manipulated bird predation pressures on entire communities than single species. The response is the sum of all spiders which means that even small effects on individual species are combined into the observed grand mortality. There were several experimental field studies of bird predation on arthropod populations in contrasting habitats between 1977 and 2007 (Table 1). In certain of these experiments the focus was on spider populations and in others, in which many arthropod taxa were studied, the results for spiders were reported separately.

Methods.—All the studies employed experimental methods using different types of exclosures to prevent birds from foraging. Typically, the exclosures covered some part the vegetation in which spiders and other arthropods were dwelling. Nearly all studies utilized nets with coarse mesh size (10–58 mm) so that arthropods were free to leave and enter the exclosures without restrictions. Possibly some large arthropods such as adult butterflies may have been hindered in their movements by the netting, but in general the authors considered such effects as negligible. In a few cases, fine mesh size (1 × 1 mm) was used but those experiments were performed during the winter when movements of spiders and their prey are usually minimal.

A factor that usually is not controlled for in most of the experiments concerns the introduction of an additional structural component to the habitat in the form of the net. This is a classical problem in exclosure experiments in other habitats and taxa (Hairston 1989). The primary disturbance caused by addition of the extra net-structure may be to support more web building spiders (Rypstra 1983; Greenstone 1984). This could increase the carrying capacity of spider populations if there is shortage of sites for attaching webs in the study habitat (Robinson 1981; Greenstone 1984; Wise 1993; Rypstra et al. 1999). However, there are reasons to believe that the bias due to the extra net-structure is rather weak. First, nearly all experiments have been performed in trees or bushes with abundant foliage (including leaves, needles, branches, twigs etc.) for attaching webs. There is, therefore, no reason to expect that structure in itself is limiting in the studied habitats, but it would be highly welcome if appropriate controls using sheets of netting (without enclosing the foliage) were included in future experiments. However, in at least one experimental study the authors used procedural

Table 1.—Field experimental studies of bird predation effects on spider assemblages. The experimental effect is shown as the ratio of density of spiders in experimental units to control units. Significance levels shown as * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$) or NS (not significant).

Habitat	Experimental season / country	Methods	Population estimate	Experimental effect: density experimental unit / density control unit	Reference
Coniferous forest (*Picea abies* trees)	Winter: October–March / Sweden	Net-enclosures: coarse (10 mm) and fine (1 mm) mesh size	No. per kg branch-mass	Coarse mesh size: 3.01 ** Fine mesh size: 1.54 *	Askenmo et al. (1977)
Broadleaf forest (understory shrub)	June–August / New Hampshire, USA	Net-enclosures (mesh size 22 mm)	No. per 400 leaves	0.96 NS	Holmes et al. (1979)
Coniferous forest (*Picea abies* trees)	Winter: October–March / Sweden	Net-enclosures: fine (1 mm) mesh size	No. per kg branch-mass	2.67 **	Gunnarsson (1983)
Temperate broadleaf forest (Pennsylvania), subtropical (Peru) & tropical forest (Gabon)	26 days experimental period, various seasons / USA, Peru, Gabon	Cages: coarse mesh size, Penn.: 30 mm (chicken wire), Peru & Gabon: 30-50 mm (sticks)	No. in experimental plots	Penn. Day: 1.20 NS, Night: 1.01 NS Peru, Day: 2.37 *, Night: 1.32 NS Gabon, Day: 1.60 *, Night 1.23 NS (survival of exp. spiders)	Rypstra (1984)
Sagebrush (*Artemisia tridentata*) up to 2 m	13 months: June 1982–July 1983 / Oregon, USA	Cages (25 mm mesh size)	No. per plant	1.64 *** (both experimental & control first defaunated)	Wiens et al. (1991)
Coniferous forest (*Picea abies* trees)	23 months: April 1989–March 1991 / Sweden	Net-enclosures: coarse (10 mm) mesh size	No. per kg dry branch-mass	Summer-89: 1.82 NS Winter-90: 3.77 *** Summer-90: 2.17** Winter-91: 2.34***	Gunnarsson (1996)
Salix shrubs	June–September / Finland	Cages, mesh size 22 mm	No. per leaf area	? NS	Sipura (1999)
Broadleaf forest (*Quercus* & *Betula* trees)	May–September / Sweden	Net-enclosures: coarse (10 mm) mesh size	No. per kg leaf mass	Oak*** site A: 1.58, site B: 6.06, site C:7.84 Birch*** site A: 5.89, site B: 8.93, site D: 3.09	Gunnarsson & Hake (1999)
Coffea arabica (shrubs, "dwarf hybrids")	January–May / Guatemala	Net-enclosures: coarse (58 mm diagonal size) mesh size	No. per 100 g foliage	2.18 **	Greenberg et al. (2000)
Eucalyptus calophylla (saplings < 3 m)	12 months: May 1997–May 1998 / Australia	Cages, mesh size 25 mm	No. per plant	August-97: 2.35 ** October-97: 2.50 ** May-98: 3.74 ***	Evelegh et al. (2001)

Table 1.—Continued.

Habitat	Experimental season / country	Methods	Population estimate	Experimental effect: density experimental unit / density control unit	Reference
Metrosideros trees, 2–3 m tall	33 months: August 1998–May 2001 / Hawaii	Cages, coarse mesh size (20 mm)	No. per 100 g foliage	0.82 NS (excluding one abundant, invasive sp)	Gruner (2004)
Inga spp, branches 3–4 m above the ground	Dry season: February–April Wet season: May–July / Mexico	Net-enclosures, coarse mesh size (35 mm)	No. per gram dry foliage	Dry season: 3.00 *** Wet season: 1.80 ***	Philpott et al. (2004)
Canopy, 30–40 m, e.g. *Anacardium excelsum, Brosimum utile, Manikara bidentata.* Understory, ≈ 1.2 m	11 months: April 2000–March 2001 / Panama	Enclosures, coarse mesh size (20 mm)	No. per m^2 leaf area	Site 1: Canopy, Wet 2.00 ***, Dry 1.60 * Understory, Wet 0.80 NS, Dry 1.10 NS Site 2: Canopy, Wet 0.85 NS, Dry 1.10 NS Understory, Wet 1.15 NS, Dry 0.60 NS	Van Bael et al. (2003) Van Bael & Brawn (2005)
Pinus trees, 1–3 m tall	27 months: June 1999–September 2001 / Colorado, USA	Cages, coarse mesh size (25 mm)	No. per tree	Hunting spiders: 1.25 * Web-spinning spiders: ? NS	Mooney & Linhart (2006)
Pinus trees, 4.5–13.5 m tall	June to September / Colorado, USA	Net-enclosures, coarse mesh size (25 mm)	Biomass estimate (mg dry spider / kg branch mass)	Hunting spiders: ? (biomass–38%) NS Web-spinning spiders: ? NS	Mooney (2006)
Eucalyptus saplings, ≤ 2.8 m tall	20 months: October 1998–May 2000 / Australia	Net-enclosures, coarse mesh size (35 mm)	No. per sapling	Nov-98: 2.05 * March-99: 2.06 * June-99: 1.77 *** Nov-99: 2.54 *** Feb-00: 2.51 *** May-00: 1.60 *	Recher & Majer (2006)
Pinus trees, branches 0.5–6.0 m above the ground	14 months: June 2001–August 2002 / Colorado, USA	Net-enclosures, coarse mesh size (25 mm)	Biomass estimate (mg dry spider / kg branch mass)	Hunting spiders: ? (biomass–24%) * Web-spinning spiders: ? NS	Mooney (2007)

controls (Van Bael & Brawn 2005). These dummy exclosures had open sides that allowed birds to forage in the foliage. There was no indication that the dummy exclosures attracted arthropods, or reduced the light. Second, birds could always reach spiders sitting in their retreats or on their webs attached to the outside or on the inside of the cage or net. This ability of birds to reach spiders just inside the exclosure, of course, depends on mesh size but nearly all studies have used a coarse mesh size which should be penetrable by bills of insectivorous birds. If spiders prefer to place their webs close to the net this could lead to an underestimate of bird predation pressure. Third, in some of the studies the effects of extra net-structures were possibly minimized by a long experimental period. For instance, if the study was performed in temperate or boreal zone with cold winters, interaction between the net-structure and spiders is probably minimal during cold periods.

The database on bird predation effects.—The studied habitats are mainly forests in different successional stages with shrubs and trees as experimental units. Coniferous trees as well as broadleaf species have been examined. Three studies were from coniferous forests in southern Scandinavia with *Picea abies* as the predominant tree (Askenmo et al. 1977; Gunnarsson 1983, 1996). The investigations focused on branches in the lower part of the canopy (up to 4 m above the ground) that were reached by using a transportable platform. Spider densities were related to the branch-mass. Three studies in Colorado were also in coniferous forest. In one case, the samples were all from rather small *Pinus* trees, not taller than 3 m (Mooney & Linhart 2006). In the other experiments, pines were between 4.5 and 13.5 m tall (Mooney 2006, 2007). The spider densities were measured as number of animals per tree (Mooney & Linhart 2006), or biomass per branch (Mooney 2006, 2007).

One early study on bird predation on arthropods was done in a broadleaf forest in New Hampshire (Holmes et al. 1979). However, the experiment was performed in understory shrubs (*Acer pensylvanicum*). In Northern Europe, Sipura (1999) investigated bird predation effects in *Salix* shrubs and Gunnarsson & Hake (1999) examined arthropods on branches in canopies of *Quercus* and *Betula* trees. A "sky-lift" was used to sample up to 6 m above the ground. In these studies, spider densities were related to number of leaves, leaf area, or leaf mass.

In five studies, moderately high trees were used for experimental purposes. Saplings of *Eucalyptus* spp. up to a height of 3 m were sampled in Australia (Evelegh et al. 2001; Recher & Majer 2006) and in these cases the number of arthropods was counted per sapling without compensation for size differences. Other investigations were done in coffee plantations, either in shrubs of *Coffea arabica* (Greenberg et al. 2000) or in branches of *Inga* trees 3–4 m above the ground (Philpott et al. 2004). In Hawaii, spider populations in 2–3 m tall trees of *Metrosideros* were examined for bird predation effects (Gruner 2004). The densities of spiders in these three studies were related to the mass of foliage.

One study was done in several rain forests in Panama (Van Bael & Brawn 2005). The height of the tree top canopies varied between 30 and 40 m above the ground and in some of the sites the predominant tree species were *Anacardium excelsum, Brosimum utile* and *Manilkara bidentata*. The tree tops were reached by using canopy cranes with a 50-m tower that had a gondola attached to a boom. In this way, the investigators could reach tree branches on all heights and each crane covered between 0.70 and 0.88 ha of the forest canopy. The arthropod densities were estimated as numbers per leaf area.

One of the studies was performed in open land in Oregon. In this experiment, plants of *Artemisia tridentata* were manipulated to examine the effects by bird predation and plant chemistry (Wiens et al. 1991). Finally, Rypstra (1984) conducted an experiment with a standardized number of spiders placed in the vegetation of a broadleaf forest in temperate, subtropical, and tropical environments. The disappearance rates of spiders were used for comparison between treatments.

The studies ranged over five geographic regions. There were five experiments performed in Northern Europe (Sweden and Finland), five in North America (New Hampshire, Oregon, and Colorado), three in Central America (Mexico, Guatemala, and Panama), one in Hawaii and two in Australia. In addition, one experiment was performed on three continents (USA, Peru, Gabon).

Five of the studies were long-term with an experimental period over 12 months and another study continued for 11 months. These investigations covered at least an annual cycle and this means that the data were not the result of a temporary predation effect. The seasonal variation in bird predation pressure could potentially be large because of variation in bird density (e.g., seasonal migration) or intensity of foraging (e.g., raising hatchlings). It has also been proposed (Askenmo et al. 1977) that bird predation could be strong during the non-breeding season because of non-favorable climate in winter. This means that non-migratory birds have to increase their efforts of finding food in winter to meet their energy demands (e.g., Norberg 1978). Some of the studies focus on the winter situation, or the dry season, and the effects on prey populations. Other studies were short-term experiments focusing on the direct effects on arthropods during summer, or the breeding season.

Experimental results at the community level.—Summarizing the data in Table 1, it can be concluded that bird predation often significantly reduces spider densities. Comparisons were based on the ratio of mean density on experimentally enclosed vegetation and controls without such restrictions. Data showed that spider densities on plants protected from bird foraging significantly exceeded controls in ratios between 1.25 and 8.93. The mean ratio for experimental tests with a significant effect was 3.03 (SD 1.93, $n = 27$). This estimate includes more than one test in each paper because many of the experiments reported were divided into separate investigations on different tree species and sites, etc. The studies included could be regarded as independent tests, although in some cases data were analyzed in an overall ANOVA. The mean ratio in tests with a non-significant result was 1.03 (SD 0.35, $n = 9$). Six studies, however, could not be included in the density ratios. Two studies (Rypstra 1984; Wiens et al. 1991) were not included because of the experimental design (see below), and in two cases it was not possible to calculate any ratio because no data were presented (Sipura 1999; Mooney & Linhart 2006). Finally, in two studies, there were no density estimates provided; instead the biomass was estimated from spider length distributions (Mooney 2006, 2007).

The data taken together could be used for a rough estimation of the percentage of experimental tests that resulted in significant effects of bird predation on spider densities. A study that reported the most dramatic effect (25–80-fold increase) was excluded because it focused on a single, invasive species (Gruner 2005). Overall, 63% of the tests indicated a significant reduction in densities of spider communities. This suggests that bird predation could be regarded as a potentially important mortality agent.

It should be noted that nearly all experiments examined report on bird predation effects in forest ecosystems or in habitats with dense vegetation of bushes, often including at least a few trees. Only Wiens et al. (1991) reports on bird predation in an open habitat with sagebrush (*Artemisia tridentata*). This could be explained in two ways: either there have been few experiments performed in open habitats, or the experiments have mostly produced non-significant results that have been difficult to publish in refereed journals. It is, of course, also possible that a number of studies performed in forest habitats have remained unpublished because they did not show any significant results. However, several studies have focused on the effects on the arthropod populations in the study habitat. This means that a large number of taxa are often analyzed, some groups showing a significant response to bird predation others showing no significant response. Possibly, this type of experimental study, which includes several arthropod taxa, reduces the risk of "hiding" non-significant results, because a significant effect by birds on at least one arthropod group often justifies publication. In published studies, spiders are often among the taxa that are numerically affected by birds. In some experiments, bird predation effects were detected in spiders but not in other arthropods, or in few other taxa. For instance, Evelegh et al. (2001) examined the effects of bird predation on 19 different arthropod orders of *Eucalyptus* saplings but they only found evidence for a significantly higher density of spiders in net-protected canopies. On the other hand, Gunnarsson & Hake (1999) found that bird predation negatively affected arthropod abundances in six out of nine orders (including spiders) examined in birch (*Betula pendula*) and oak (*Quercus robur*) canopies.

The experimental studies by Rypstra (1984) on predation (predominantly by birds) on web-building spiders in three continents, and by Wiens et al. (1991) of bird predation on arthropods in sagebrush (*Artemisia tridentata*) were not included in the mean value of predation effects reported above. The reason for excluding them is that the comparison was not based on control vs. experimental density. In Rypstra's study (1984), a fixed number of spiders (240 individuals in four groups in each of the study sites) were placed in forest sites and their survival during 6-h periods was measured. Thus, there was no estimation of the natural density, or the effect on the spider community. However, Rypstra (1984) could show that the relative disappearance rate of spiders was higher during the daytime than at night at the Peru (subtropical forest) and Gabon (tropical forest) sites but not at the site with temperate forest in the USA. She concluded that predation by vertebrates (most likely birds) was significant on web-spiders during the daytime in subtropical and tropical sites.

Wiens et al. (1991) used an approach that differs from all other experiments reported on here; i.e. arthropods were first removed from shrubs and the recolonization of different taxa on caged or exposed shrubs was observed. No exact calculations for arachnids were given in the text. However, raw data provided in the paper's Appendix 1 could be used to assess the importance of bird predators on the abundance of spiders on sagebrush. The relevant comparison is the one between shrubs that were caged and open shrubs because both types of shrub were defaunated at the same time and the only difference was caging. Wiens et al. (1991) used several sub-experiments in their design and the longest experimental period was 56 weeks. The mean value for caged shrubs after 56 weeks was 1.89 spiders and for open shrubs the mean was 1.15 spiders. This difference was significant ($P < 0.001$) using a *t*-test. Consequently, the experimental result supports the hypothesis that birds affect the abundance of spiders in sagebrush.

BIRD PREDATION ON SINGLE SPECIES

Studies of ecological mechanisms can be difficult to perform on communities because the various species respond in very different ways. Therefore, experimental investigations on bird predation effects on single species may reveal how the predation affects life-history traits. There are few studies focussing on the effects of bird predation on a specific spider species or genus. Here, I will review four studies that employ experimental methods. The first study concerns the funnel-web spider *Agelenopsis aperta* (Gertsch 1934) in two distinct habitats in Arizona (Riechert & Hedrick 1990). The funnel functions as a retreat that protects the spider from predatory attacks.

The two study sites included a desert grassland and a riparian habitat in woodland, respectively. In their study, Riechert & Hedrick (1990) estimated predation rates on *A. aperta* in two ways. First, in each study site an area of 900 m^2 was enclosed with sheet metal flashing. All spiders in webs were marked and pitfall traps at regular intervals inside and outside the metal flashing made it possible to detect migrating individuals that were marked and released on the opposite side of the metal flashing. Second, a field experiment was performed by protecting certain webs from bird predation by means of netting. The survival of individuals at protected webs was compared with those at unprotected webs in 1-week periods.

In the population monitoring, the losses of individuals differed significantly between the habitats. In the riparian site, spiders disappeared at a rate of 63% to 72%. However, in the grassland area, the disappearance rate varied between 4% and 10%. The experimental exclusion of bird predation resulted in large differences in disappearance rate (30% and 51% difference per year) between protected and unprotected webs in the riparian habitat, with higher survival of spiders in protected webs. In the grassland habitat, there were no significant differences in spider survival at protected and exposed webs. Consequently, bird predation on *A. aperta* seemed to be important in the riparian habitat but no measurable effect could be found in the grassland. Riechert & Hedrick (1990) also referred to a study by Greene (1989) that reported significant bird predation effects on canopy-living spiders in a pine habitat adjacent to their riparian habitat.

Vertebrate predation on two species of lycosids, *Schizocosa ocreata* (Hentz 1844) and *S. stridulans* Stratton 1984 was studied in an exclosure experiment in secondary forest in Kentucky (Wise & Chen 1999) over two years. These wolf spiders were very common on

the floor of forests dominated by oak and maple and > 90% of lycosids in the study site belonged to the genus *Schizocosa*. Birds and other potential vertebrate predators, such as shrews, were common in the experimental plots. In late spring, five locations were established. In each location, two 50 m^2 areas were selected at random as a "removal-exclusion" treatment, or as "open reference." Vertebrates inside each exclosure were trapped and removed. The density estimates of *Schizocosa* included all stages and the analysis was based on eight samples during two years.

The removal of vertebrate predators, including birds, did not affect lycosid densities. The treatment factor (i.e., the exclosure) approached $P = 0.10$ in an ANOVA but *Schizocosa* densities tended to be higher in the "open reference" plot rather than the protected one. Wise & Chen (1999) suggested that the removal of vertebrate predators might cause an increase in the density of another, unknown major arthropod enemy of *Schizocosa* that depressed the lycosid density. However, they emphasized that this was a speculative suggestion.

In a study during two years, the effects of bird predation on the linyphiid *Pityohyphantes phrygianus* (C.L. Koch 1836) was examined by manipulation of predation pressure (Gunnarsson 1993, 1998). This sheet-web spider lives on branches of coniferous trees and it is exposed to predation by passerine birds during all stages of the biennial life cycle. Many of the bird species are non-migrating and they form multi-species flocks that patrol the same area during overwintering.

The results were part of an experiment on bird predation effects on the spider community in spruce (Gunnarsson 1996). Randomly selected spruce branches between 1.5 and 4 m above the ground were enclosed in coarse-meshed nets (mesh size 10 × 10 mm) and other branches were left as controls. Four sampling periods, fall and spring in each of two years, were used and in all cases removal of bird predation significantly increased the density of *P. phrygianus*.

In the spring samples, i.e., after the winter period with a combination of bird predation and other, temperature related, mortality causes, the spider mean density of experimental, net-enclosed, branches was 4.1–10.5 times the mean of control branches (Gunnarsson 1993). In samples collected in the fall, the mean densities in net-enclosed branches were 2.3–2.6 times the densities of controls. The predation effects on males and females were similar in three out of four samples (Gunnarsson 1998). In the fall samples, the mean number of individuals for each sex on net-enclosed branches was 2.1–2.3 times the controls. A more pronounced difference between the two branch categories was found after the winter. The mean number of males on protected branches was 10.3 times the controls, and for females the effect was 10.6 times. However, in the second spring sample there was a sex-related difference in the bird predation effect. In males, there were 5.5 times more individuals on net-enclosed branches compared with control branches. In females, the predation effect was only 2.8 times more individuals on protected branches. These results suggest that bird predation can be sex-specific under certain circumstances and this will be discussed further below (see "Selective predation").

Another experimental study of bird predation was carried out on a theridiid spider, *Achaearanea* cf. *riparia* (Blackwall 1834) on the island of Hawai'i. This species is an exotic to the study site and it is presently expanding its distribution on several locations on the island of Hawai'i (Gruner 2005). The experimental site was a high altitude, wet forest in early succession and the vegetation was dominated by the tree *Metrosideros polymorpha*. Birds were common insectivores in the study site.

The results on *A. riparia* were part of a larger experiment that examined the relative influences of bottom-up and top-down effects in a Hawaiian food-web (Gruner 2004). Fifteen individuals of *A. riparia* were collected in total from 28% of the plots at the start of the study. However, at the end of the experiment, 939 individuals were collected in caged plots but only 22 individuals in control plots where birds could continue their foraging without any restrictions. If the abundance is expressed as spider density (No. per 100 g foliage), the mean density on caged trees was approximately 28 times the mean density on control trees. A closer look at the size distribution of *A. riparia* in the treatment groups suggests that large individuals benefited even more from exclusion of bird predation. The possible size selection by birds on spiders will be discussed now.

SELECTIVE PREDATION

Bird predation pressure on spider populations can have consequences that are much more far-reaching than just a reduction of the local abundance. If bird predators select their prey with some sort of discrimination there will be unequal risks of being eaten depending on the phenotype of the prey. This will lead to a selective advantage to certain individuals and over time the frequencies of different phenotypes in the population will change due to bird predation. The prerequisites for such a process are (i) variation in the studied trait (size, color, etc.), (ii) a genetic basis for the trait, and (iii) fitness differences between individuals displaying the trait. When these conditions are fulfilled, natural selection occurs (Endler 1986).

There are several studies on birds acting as selective agents on their prey. Especially birds in forest ecosystem may have a large evolutionary impact on their arthropod prey (Holmes 1990). There are a number of studies of predation effects on spider populations that can be used to assess the importance of birds as selective agents. In reviewing these studies, I put special emphasis on the experimental evidence but in certain cases I also include investigations in which there are good reasons to assume bird predation as an important mortality factor.

Selection on size, sex and color.—One of the most obvious traits for selection is size. Theoretical models suggest, for instance, that size-specific predation pressure can affect the evolution of life history if the coupling between predator and prey is strong (Day et al. 2002). Size is an extremely important trait that affects many aspects of the life history of spiders and other arthropods. Data suggest that females of the agelenid *Agelenopsis aperta* can benefit in terms of fitness by mating with a large male (Riechert & Johns 2003). The offspring of females mated to large males were "bolder" and more aggressive than the offspring sired by small males. There are numerous studies showing that large males have a higher probability of winning contests with smaller opponents over females (see Elgar 1998 for examples). Moreover, in some species large males mature early and this is favored if there is protandry, i.e., males on average maturing before the females (e.g., Gunnarsson & Johnsson 1990). If there is first-sperm priority, which is common in many spiders (Elgar 1998), the males reaching the adult stage early will have a mating advantage. This could be achieved by enhanced growth rates and large size, which suggests that sexual selection is acting (Wiklund & Fagerström 1977; Gunnarsson & Johnsson 1990), but early maturation could also be associated with small size and fewer molts (Vollrath 1987). In addition, it should be noted that in many species there is obviously selection for small male size because of predation risk (e.g., Vollrath & Parker 1992). In female spiders, there is a general relationship between large size and fecundity (Vollrath 1987; Marshall & Gittleman 1994). This has been suggested as a major selective force for the evolution of size dimorphism exhibited in several spider genera, e.g., *Nephila* (Coddington et al. 1997). However, predation by visually hunting predators is potentially an important selective force acting against large size.

Experiments on bird predation effects on the entire spider population in a forest ecosystem have often revealed that there are differences in predation pressure on various size categories. For instance, in a coniferous forest in Sweden there was a significant decrease in population size by large spiders (body length $\geq$ 2.5 mm) but this was not found for small spiders during winter (Askenmo et al. 1977). In the same system, Gunnarsson (1983) found a significant decrease in the density of both small ($<$ 2.5 mm) and large ($\geq$ 2.5 mm) spiders during winter but bird predation pressure varied. A comparison of spring densities expressed as the ratio between experimental (branches protected from predation) to control mean density showed that for small specimens there was a 2.0-fold increase in density on branches protected from bird predation. The increase in the number of large specimens on protected branches was 6.1. This suggests that the predation pressure on large spiders was higher than on small ones.

In another experiment in a spruce (*Picea abies*) forest of southern Sweden, the mean (and median) size was significantly larger on branches protected from predation via exclosures (Gunnarsson 1996). The experiment started in spring and the first sampling was done in fall, five months later, and the second sampling was performed after the winter, six months after the first one. Another two samplings were executed in fall and spring with a six-month interval

between. In all samplings, the mean size of spiders on branches protected from bird predation was significantly larger than on unprotected control branches. The mean size of spiders inside exclosures was 133% and 124% of the size on control branches exposed to predation in samples after the summer. In early spring, after the winter, the corresponding differences were 132% and 133%, respectively. Thus, removal of bird predation increased the mean size with 24–33%, suggesting that birds were selecting large-sized spiders as prey in both summer and winter. However, there was a reduction in mean size in control branches after winter in comparison to fall samples (2.42 to 1.79 mm and 2.29 to 1.87 mm).

In an exclosure experiment, Recher & Majer (2006) examined the effects of bird predation on arthropods in *Eucalyptus* woodland. The spiders were categorized into three size-classes (i.e., size-class 1: ≤ 2.0 mm, size-class 2: $> 2.0 \leq 4.0$ mm, size-class 3: > 4.0 mm) and densities inside and outside exclosures were compared six times during 1.5 years. In size-class 1, the densities were significantly higher on enclosed saplings than on controls in five out of six comparisons. In the two larger size-classes, 2 and 3, there were significantly higher densities in four out of six and two out of six comparisons, respectively. Overall, when averaged over the six samplings the ratios for densities on enclosed saplings over control branches of the size-classes 1, 2, and 3 were 2.2, 1.8, and 2.5, respectively. This suggests that bird predation effect was high in all size-classes, but low abundances and high variances, in particular in the largest size-class, resulted in few significant differences between experimental and control branches.

Studies on single species also show that birds are a stronger selective agent on large individuals in comparison with smaller individuals in *Pityohyphantes phrygianus* (Gunnarsson 1998). In a temperate forest, overwintering subadults that did not molt between the samplings in fall and spring in two years were examined in an experimental study. Large individuals survived better than smaller ones in both sexes and both years. In March each year, the mean size ratios of females on net-enclosed branches versus controls were 1.07 and 1.05, respectively. In males, the ratios were 1.09 and 1.02 (not significant), respectively. Consequently, passerine birds in the coniferous ecosystem studied seemed to catch disproportionately more large individuals of female and male *P. phrygianus* during winter.

In the invasive *Achaearanea* cf. *riparia* on the island of Hawai'i (Gruner 2005), comparisons of the total abundance of five size-classes suggested that the intensity of bird predation was lowest on the smallest size-class (individuals between 0.5 and 1.5 mm). There were no individuals larger than 3 mm found in control plots, whereas 34 spiders 4 or 5 mm long were collected within cages that protected *M. polymorpha* trees from bird predators. Given the few individuals collected in certain size-classes, no statistical test was performed. This means that the data are supporting the hypothesis that birds were size-selective, but no firm conclusion could be drawn.

Selection on size is closely related to sex-specific survival. Sexual size dimorphism is common in several families; e.g., Araneidae (Foelix 1996; Roberts 1996), and the evolution of spider size dimorphism has been much discussed (Vollrath & Parker 1992; Coddington et al. 1997; Vollrath 1998; Prenter et al. 1997, 1999). For instance, in web-builders it has been argued that males spend more time searching for females that are often sedentary in their webs. This means that the sexes may have differences in exposure time to visual predators and this could select for smaller size in the roving males (Vollrath & Parker 1992).

There are several studies indicating that males move around to a higher extent than do females of web-building spiders, but the experimental evidence of a higher predation pressure on males is meagre. Individuals of *Theridion grallator* Simon 1900 that moved around in forest habitats were caught on leaves coated with adhesive (Gillespie & Oxford 1998). From December through February only immatures were collected. In the period between March and August nearly all individuals were males but no mature female was caught at all. This suggested that males were more vagrant than females. However, females of web-builders in other species may move between different sites to change the location of the web. In the orbweaving *Tetragnatha elongata* Walckenaer 1842 the frequency of relocation depended not only on habitat quality (prey capture rates) but also on the distance travelled between the habitats (Gillespie & Caraco 1987). The distance moved at the site with few prey was 2.8 times the distance travelled at the site with high

captures rates. However, there may also be sex differences in distance moved in free-hunting spiders. For instance, males of *Hogna helluo* (Walckenaer 1837) moved nearly 3 times further than females in a laboratory experiment (Walker & Rypstra 2003). However, such a difference was not found for *Pardosa milvina* (Hentz 1844).

The survival of males and females has been examined in certain spiders and the mortality rates could sometimes be related to predation by birds. An estimation of mortality in *Nephila clavipes* (Linnaeus, 1767) in Panama (Vollrath & Parker 1992) showed that roving males experience a much higher risk of death (> 80% in 10 days) than females, subadults or juveniles, i.e. from ≈ 7% in 20 days in mature females to ≈ 30% in subadult females. There appears to be a switch in male mortality, from relatively low to considerably higher death rates, when they mature and start searching for sedentary females. Part of the lower survival of males is probably related to increased exposure to visually hunting predators such as birds. Moreover, moving in itself is risky and increases the probability that active spiders will be eaten by birds (Avery & Krebs 1984).

In *Pityohyphantes phrygianus*, experimental evidence from Scandinavian forests show differential mortality of the sexes. A combination of factors contributes to the skew in mortality rates. In a series of experiments focusing on the winter survival of subadults it was shown that males were more vulnerable to various mortality factors. First, males were more susceptible to low winter temperatures than females (Gunnarsson 1987b). In a field experiment, the cold-induced component of winter mortality was examined. Male survival (48%) was significantly lower than female survival (81%). This was supported by a significant correlation between change in the proportion of males in the study population and mean temperature in February (Gunnarsson 1987b); the lower the temperature, the higher the reduction in proportion of males in the population. Second, in a laboratory experiment at low temperatures, males increased their activity significantly when the ambient temperature was raised from +5 °C to +10 °C (Gunnarsson 1987b). Females did not respond to such a temperature increase. Consequently, males became more active during warm winter days, which occurs frequently during winter in SW Sweden, and thereby expose themselves to hunting passerines. Third, in a 2-year field experiment the selective predation by birds on male and female *P. phrygianus* was studied in southern Scandinavia (Gunnarsson 1998). In one of the winters investigated, the predation pressure by birds on male spiders was stronger than on females. Males were affected by a predation pressure that was approximately twice that on females. As a result, the population sex ratio in spring differed significantly between branches protected from bird predation and control branches. On net-enclosed branches there were 34% males vs. 13% males on control branches. The normal sex ratio in Swedish forests is ca. 33% males (Gunnarsson 1987b, 1989) and this also applies to the primary sex ratio (Gunnarsson & Andersson 1992). In the other winter studied, the sex ratio did not differ significantly from the primary sex ratio (Gunnarsson 1998).

In a field experimental study, the survival of the sexes of two lycosid spiders, *Hogna helluo* and *Pardosa milvina*, was compared (Walker & Rypstra 2003). Researchers tested the hypothesis that there is a correlation between life-style and mortality, as suggested by Vollrath & Parker (1992). The two lycosids examined differed in their sexual size dimorphism and activity but they occurred in similar habitats (soybean fields in the present case). The experimental design of the study included an estimation of sex-specific survival in aluminium flashing exclosures with known numbers of individuals added. However, all the exclosures had open tops, so both invertebrate and bird predators could attack spiders during the entire study (1 or 2 weeks depending on species). Walker & Rypstra (2003) found significant differences in *Pardosa*, where males suffered from a higher mortality than females, but not in *Hogna* survival. The result was, however, not in agreement with the Vollrath-Parker (1992) hypothesis because *Hogna*, but not *Pardosa*, showed a significant difference in activity so that males moved longer distances than females. It is also possible that bird predation mainly acts on *Pardosa* because they are day-active but *Hogna* is a nocturnal species (Walker & Rypstra 2003). Why there was a survival difference between the sexes of *Pardosa* in this study remained unexplained.

The maintenance of color polymorphism is often attributed to frequency-dependent preda-

tion. For instance, the common color morph will be eaten disproportionately often by visual predators and this will maintain a polymorphism in the population (e.g., Allen 1988). In certain spiders, color polymorphism has been described and different types of balancing selection have been shown to be involved in the maintenance of the color morphs (Oxford & Gillespie 1998). It has also been suggested that there are female-biased color polymorphisms in spiders that could be maintained by differential bird predation (Stamps & Gon 1983). However, no data have been presented to support this hypothesis. Only a few studies have attempted to test the importance of bird predation on color variation in spiders. Studies on the Hawaiian happy-face spider *Theridion grallator* showed that balancing selection affected the color morph frequencies and apostatic selection by bird predators was offered as an explanation (Gillespie & Oxford 1998). However, no actual tests were performed, although moving individuals of *T. grallator* were caught during one year. Few individuals (18) were trapped in sticky coating on the underside of leaves. Five individuals were immatures and the rest were adult males. Possibly, this suggests that males are more vulnerable to bird predation because their frequent movements puts males at higher risk for detection (Avery & Krebs 1984).

In *Pityohyphantes phrygianus* there is continuous variation from pale to dark color, probably caused by polygenic inheritance (Gunnarsson 1987a). Melanic individuals were shown to be more active at low temperatures than individuals with paler coloration. This suggested that melanics should be more vulnerable to bird predation during winter when some activity by *P. phrygianus* occurs on suitable days with temperatures between 4 and 10 °C (Gunnarsson 1985). Data from a large field experiment (Gunnarsson 1996) with spruce branches protected from bird predation were used to evaluate this hypothesis (Gunnarsson 1993). However, no support for differential survival of color morph was found in this experiment. It should be noted that melanics usually only make up between 3% to 4% (range 1% to 8%) in the natural population (Gunnarsson 1987a) which makes it difficult to establish significant changes in the population due to sampling error.

Selection on behavior and species composition.—The risk of a spider being eaten by a bird may depend on the individual's behavior. Important aspects of the behavior of spiders are often related to the species, genus, or family. Hunting strategies, for instance, divide families into web-building and free-hunting, or cursorial, spiders. Web-builders could further be divided into several sub-groups depending on web architecture. Blackledge et al. (2003) suggested that predators, mainly sphecid wasps, have been important selective forces for the evolution of three-dimensional webs as a defense against such predation. So, if visually hunting predators exercise a strong selective pressure on spiders, there should be many aspects of spider biology that could be attributed to such selection. Indeed, there seems to be evidence for this conclusion. One example could be the vast variation and complexity of anti-predator devices, which have been comprehensively reviewed by Cloudsley-Thompson (1995) for spiders in general and by Edmunds & Edmunds (1986) for West African orb weavers. The studies reviewed below have examined the effects of bird predation on differences in behavior, including selective predation on the various families, in experimental investigations.

Avery & Krebs (1984) showed in aviary experiments that active spiders were at higher risk of being eaten by Great Tits (*Parus major*) than sedentary spiders. Individuals of *Zygiella x-notata* (Clerck 1757) were released at each of 15 points in the test cage. Trials lasted for 10 min and tests were performed at 2–13.5 °C. Previously, spider activity had been measured at 2–20 °C. There was a good agreement between bird capture rate and spider activity. At low temperatures (2–7 °C) spider activity was low and few spiders were captured. However, both capture rate and spider activity increased rapidly when temperature increased from 7 to 9–10 °C. Above 10 °C, there were only minor increases in capture rate and activity.

In a study of *Agelenopsis aperta*, Riechert & Hedrick (1990) examined anti-predator behavior in two populations (see details above, "Bird predation on single species"). They found that individuals that were experimentally disturbed in their webs reacted differently in the two populations. Grassland spiders that experienced low bird predation pressure returned significantly faster to their funnel entrances after disturbance than did spiders at the riparian site. The bird predation pressure was

strong in the riparian habitat (see above). This difference in anti-predator behavior was also found in second-generation laboratory-reared individuals. This is strong evidence that birds can affect the evolution of behavioral traits in spider populations.

One specific behavior that deserves to be mentioned is the construction of webs. It is possible that birds use webs in the vegetation as an indicator of the presence of spider prey. There are observations in the wild of birds hovering close to webs and capturing spiders (e.g., Edmunds & Edmunds 1986). It has been argued that inclusion of stabilimenta could function as visual advertisement so that predators such as birds could avoid accidentally flying into sticky webs (Eisner & Nowicki 1983). In field experiments, some webs spun during night were artificially marked with white paper cut to resemble an X-shaped stabilimentum. Other webs were left untouched as controls: in both cases the resident spiders were removed. The persistence of webs was then followed during the day. By noon there was a highly significant difference between the web categories. Most of the unmarked controls were destroyed, only 8% were left, whereas > 60% of the artificially marked webs were still intact. In another experiment, Horton (1980) could show that birds preferred to take *Argiope* spp. outside the web rather than on the web and that spiders on webs without stabilimenta were taken more often than spiders with stabilimenta. However, stabilimenta clearly could have a number of functions such as predator-defense, camouflage, prey attraction, etc. (e.g., Robinson & Robinson 1970; Eberhard 1973; Edmunds 1986; Schoener & Spiller 1992; Blackledge 1998), but this review will not cover aspects on this particular issue.

The hunting behavior of spiders is more or less fixed. This means that spider foraging categories often correspond with genus, or family. Consequently, a way to study the evolution of behavior is to examine families with differences in hunting behavior (see e.g., Shear 1986; Vollrath 1988). Here I summarize two studies on the impact of bird predation on different spider families.

In a field experiment (details given above, see also Gunnarsson 1996), Gunnarsson (1995) examined the relative abundance of certain families on spruce branches that either were net-enclosed (mesh size 10 mm) or controls without nets. Sampling was done in the fall and spring during two years and there was special focus on the overwintering populations. Families Clubionidae, Thomisidae, Linyphiidae represented free-hunting (C, T) and web-building spiders (L), respectively. The relative abundance was used in this study, so changes between families suggest that they were favored, or disfavored, in some way because of bird predation. This does not necessarily suggest that birds directly affect the different spider families in spruce trees because other factors, such as competition, or interspecific spider predation, could be involved. A re-analysis of the three families, plus several other families, using density data based on numbers per branch-mass, showed that free-hunting spiders as Clubionidae, but not Thomisidae, were affected negatively by bird predation (Gunnarsson, unpubl.). Web-builders such as Linyphiidae had a higher relative abundance on control branches. This could be a result of changes in competition between different families and of methodological problems. For instance, low densities of clubionids perhaps facilitated web construction of linyphiids. On the other hand, enclosing branches with net-sacks might have modified the micro-habitat on branches so that web-building was more difficult. The re-analysis of family densities suggested that both free-hunting and web-building families were directly affected by bird predation (Gunnarsson, unpubl.).

In another experiment, insectivorous birds were excluded by means of cages in ponderosa pine (*Pinus ponderosa*) (Mooney & Linhart 2006). The reason for doing the experiment was to examine differences in the strength of trophic cascades in arthropod communities in pine and its parasite, dwarf mistletoe (*Arceuthobium vaginatum*). The experiment continued for three years and arthropods were sampled by visual counting on pine branches and foliage. Seven categories of arthropods were sampled: among them hunting spiders (Salticidae and Anyphaenidae) and web-spinning spiders (Theridiidae) were recognized. The main result was that birds had no effect on growth of pine and mistletoe via predation on predatory arthropods, for example, hunting spiders, and foliage-chewing herbivores that were not tended by ants. The predatory arthropods increased their predation pressure on herbivores that were protected against bird predators. So, the

predatory arthropods compensated for the loss of bird predation. However, pine growth was significantly reduced when birds were hindered from feeding upon aphids. This occurred only if tending ants were present because they protected the ants against arthropod predators. This produced a linear food chain from birds via sap-feeding aphids to pine, whereas the reticulate food web involving predatory arthropods (including hunting spiders) and herbivores other than aphids did not produce a trophic cascade. The hunting spiders (Salticidae and Anyphaenidae) were part of the linear food chain and they were significantly affected by bird predation. However, the abundance of web-builders (Theridiidae) did not respond to removal of bird predators.

Similar results were obtained in successive experiments (Mooney 2006, 2007). Abundances of hunting spiders were affected negatively by bird predation but web-spinning spiders were not (Mooney 2007). The presence of ants affected the study system and the interactions between spiders and ants were sometimes stronger than interactions between spiders and birds (Mooney 2006).

DISCUSSION

What general conclusions about bird predation on spiders can be drawn from the present data? Lawton (1999) was rather pessimistic about the possibility to formulate conclusions in ecology in the form of "general laws." This is especially problematic in community ecology where many species interact, making attempts to generalize about ecological processes more or less impossible. It means that contradictory results could be expected when reviewing community ecology work and that site-specific environmental conditions as well as seasonal variations can have large influences on ecological processes. The literature about bird predation on spiders is mainly within "community ecology."

There is no reason to expect that bird predation on spiders is an important ecological process in all combinations of time and space. Nevertheless, the data collected in this review showed that birds generally are important predators on spiders in forest habitats whereas effects in open ecosystems, such as grassland, were not well investigated. Canopy-living spiders were especially affected by birds, but ground-living species did not show any strong response to bird predation. Part of the reason why ground-living spiders did not seem to be strongly influenced by birds could be that few investigations have tested this hypothesis. However, field experiments have shown that predation by birds can depress other arthropod populations in grasslands (Joern 1986; Bock et al. 1992). For instance, the density of adult grasshoppers in plots with exclosures was > 2.2 times the density in control plots and for nymphs the effect was even stronger (Bock et al. 1992).

Table 2.—Bird predation effects on arthropod taxa in field experiments. Effects are given as mean percentage difference in density between exclosures and controls. Only statistically significant differences are included. Data taken from Holmes et al. (1979), Gunnarsson & Hake (1999), Evelegh et al. (2001), Van Bael et al. (2003), Recher & Majer (2006), and Mooney (2006, 2007).

Taxon	Mean percentage difference	*n*	Range
Dermaptera	2687	1	–
Opiliones	1248	1	–
Heteroptera	593	1	–
Neuroptera	450	1	–
Lepidoptera	398	4	43–1200
Psocoptera	393	2	207–578
Coleoptera	254	2	76–432
Blattodea	201	2	98–304
Homoptera	195	2	103–287
Araneae	194	4	92–390
Hymenoptera	106	2	79–133
Diptera	58	1	–

Insectivorous birds may perform "ecological services" by eating pests but they also consume a lot of predatory arthropods that could be regarded as beneficial to humans. It is even possible that birds prefer certain arthropods, such as spiders, because they have high nutritious value and they do not, as far as we know, emit defensive chemicals that might be toxic or unpleasant to vertebrate predators. If spiders were preferred over herbivorous insects, the "ecological service" done by birds could be reduced.

A tentative test of this idea was performed by comparison of data on bird predation effects reported in seven studies. The data used were taken from investigations where density data for many arthropod taxa were given (Table 2). I included only taxa that had a statistically significant response to bird predation and data

were restricted to arthropods living in tree canopies to make the results from different studies comparable. The difference between arthropod density on foliage protected from bird predation and controls was given as per cent change. Following Van Bael et al. (2003), it was calculated as [(density on protected branches − density on controls) / density on control] × 100. Only one estimate per taxon and study was used, so if many estimates were available for a taxon, an average was calculated. The obtained values indicated how much removal of bird predation changed the density of each taxa. This could be used as an indirect assessment of birds preferences regarding prey. The higher the percentage change, the more that prey was preferred by the birds.

The available data suggested that spiders were not top-ranked among the taxa (Table 2). Thus, using the present data-set, there was no indication that birds prefer spiders to other arthropod prey taxa. However, it should be noted that spiders and lepidopteran larvae were significantly affected in four studies. This suggests that these two common taxa were often affected by bird predation in forest canopy systems. In the other taxa, the effects were shown in one or two studies, suggesting that the response to bird predation was dependent on specific conditions and occasionally the predation pressure lead to reduced prey density. Although the data were biased towards forest ecosystems, there was no strong indication that bird predation on spiders "reduced" the ecological service done by birds on pest insects. There is at least one experimental study that examined the impact of bird predation in combination with spider predation on lepidopteran caterpillars (Hooks et al. 2003). In a *Brassica* agroecosystem, there was significantly higher productivity in plants that were protected by predators. However, birds and spiders together did not reduce caterpillar densities more than did either predator alone. It was also concluded that birds were the most important predators on the caterpillars in the study system (Hooks et al. 2003).

The influence of bird predation on species number and diversity of spiders is still not completely known. In one experiment the number of spider morphospecies increased on *Eucalyptus* saplings protected from bird predation (Evelegh et al. 2001). Results from spider communities in coniferous trees suggest that different guilds and families could show different responses to predation by birds. The relative abundance of large hunting spiders (Clubionidae) increased in the absence of predation in spruce branches (Gunnarsson 1995). Similar results were obtained in pine trees where hunting spiders (Salticidae, Anyphaenidae) were affected negatively by birds whereas web-building species (Theridiidae) were unaffected (Mooney & Linhart 2006). Blackledge et al. (2003) suggested that hunting behavior may influence the risk of being captured by birds. If this hypothesis is correct, then hunting spiders without web and/or retreat should suffer more from predation than web-building spiders. This hypothesis, however, is not yet well tested in predator-prey systems with spiders and birds. It is also possible that the interaction between bird predation and microhabitat structure affects spider species richness (e.g., Gunnarsson et al. 2004). Further field experiments will help to elucidate the relationship between bird predation and spider species richness and diversity.

The impact of vertebrate predation on spider diversity has been examined in tropical archipelago systems with lizards as top predators. In their study, Spiller & Schoener (1998) found that spider species richness declined when lizards were present. In particular, large and rare species were negatively affected by predation whereas the impact on common species with smaller size was not statistically significant. Moreover, the mean body size of *Argiope argentata* (Fabricius 1775), a relatively rare species in the system, was much larger in the exclosures without lizards than in controls. A similar effect could be expected for bird-spider interactions given that the bird predation pressure on large spiders is higher than on small spiders in both community studies (e.g., Gunnarsson 1996) and single species studies (Gunnarsson 1998; Gruner 2005). Consequently, it could be predicted that intensive bird predation on spider communities will lead to low species richness and large-sized species should be the most vulnerable. This could lead to a trophic cascade if the birds and spiders are part of a linear food chain (Mooney & Linhart 2006). Again, only well designed field experiments will help to examine this hypothesis.

The abundance of ants in tree-canopy systems can influence the bird-spider interaction because ants are competitors to both

spiders and birds. In a boreal forest in northern Scandinavia, Haemig (1992) found that birds spent more time foraging in trees where ants had been experimentally removed than in trees with ants present. Moreover, insects and spiders had higher biomass in trees without ants (Haemig 1994). This means that birds and ants in spruce and birch trees of boreal forests may compete for a common resource, i.e., other arthropods. However, ants may also interact with spiders. In an experimental study in Oregon, Halaj et al. (1997) showed that competition can occur between canopy-living ants and spiders in Douglas-fir (*Pseudotsuga menziesii*). Although the abundance of hunting spiders (mostly Salticidae) increased significantly in trees without ants, web-building spiders (e.g., Theridiidae, Araneidae, Linyphiidae) did not respond numerically to ant removal. Interference competition was the most likely explanation for the variation in hunting spider density between treatments because ants included spiders in their diet to a low extent only (≈1% of the prey). These results indicated that future studies of bird-spider interactions should include ant density as a "covariate" in the analysis of spider abundance. Mooney (2006, 2007) has recently shown that spider - ant interactions can influence bird predation effects on spider populations. The relationship between bird predation and spider abundance may not be as straightforward as generally assumed in earlier studies.

The demonstration of bird predation as a potentially important selective force on spiders and other arthropods in forest ecosystems leads to several important conclusions. Holmes (1990) pointed out that birds are important and significant selective forces on forest arthropods. The evolution of anti-predator traits that many spiders show (e.g., crypsis and escape behaviors), should be strongly influenced by bird predation in forest ecosystems. This hypothesis is not well examined in field experiments except for a few studies on coloration (see review by Oxford & Gillespie 1998) and anti-predator behavior in *Agelenopsis aperta* (Riechert & Hedrick 1990). The study of *A. aperta* is an example of direct effects of bird predation in combination with trait-mediated effects via changes in behavior. There are probably many important indirect trait-mediated effects that affect spider populations (see Werner & Peacor (2003) for a review on trait-mediated effects). This needs to be examined in future studies. Moreover, the hypothesis that three-dimensional webs protect araneoid sheet weavers from wasps but that birds are of minor importance as selective agents (Blackledge et al. 2003) should be tested experimentally. It is important that several types of ecosystems are included in such experiments because the data presented in the present review show that bird predation pressure is strong in forest systems whereas the importance in open habitats is not yet sufficiently well known.

Another hypothesis that has received much interest in recent years is the evolution of sexual size dimorphism in spiders. The model by Vollrath & Parker (1992) assumes that small, roving males in web-building species have a significantly higher mortality than large, sedentary females. Body size was assumed to be a target to selection in this model. Some credence to this assumption was given by a field experiment to examine winter survival of *Pityohyphantes phrygianus* as males survived at lower rates during one of two winters (Gunnarsson 1998). On the other hand, selection acted against large size in both sexes when subjected to bird predation. It should be noted that in linyphiids the males are large and sometimes larger than females.

Male survival rate in the field was not correlated with body size in the lycosid *Hygrolycosa rubrofasciata* (Ohlert 1865) but males that showed high drumming rates while courting females survived better than males with lower drumming rates (Kotiaho et al. 1999). Foellmer & Fairbairn (2005) found no evidence for the hypothesis that small male size should be selected for during mate search. On the contrary, large males were most successful in one of two populations of *Argiope aurantia* Lucas 1833 studied. Furthermore, in the nephilid spider *Nephila plumipes* (Latreille 1804) male survival was very low (34%) during the search for females and there was no correlation between male mortality and body size (Kasumovic et al. 2007). In these three studies, there were no indications of what predators caused the mortality.

Another problem might be that hypotheses regarding the evolution of sexual size dimorphism have been tested in systems with ongoing reproduction. The selective forces outside the mating season have generally been neglected although the evidence suggests that predation

pressure from birds is very strong during winter, at least in temperate coniferous forest (e.g., Askenmo et al. 1977; Jansson & von Brömssen 1981; Gunnarsson 1983, 1996). This is potentially important because the sexes may respond differently to environmental conditions, such as food availability, outside the mating season (Gunnarsson & Johnsson 1990). More studies are needed to elucidate the role of bird predation as a sex-selective force during mating season but also during other seasons.

The lack of details regarding selective agents in many recent selection studies calls for new field experiments. In the light of the present review, bird predation is a highly probable selection pressure on spiders in many contrasting forest ecosystems. A combination of several types of studies – descriptive, laboratory and field experiments – will lead us forward in better understanding the ecological mechanisms involved in interactions between birds and spiders and it will also tell us something about the evolutionary consequences on spider populations.

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SHORT COMMUNICATIONS

JUVENILE *NEPHILA* (ARANEAE, NEPHILIDAE) USE VARIOUS ATTACK STRATEGIES FOR NOVEL PREY

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ABSTRACT. *Nephila clavipes* (Linnaeus 1767) and *N. pilipes* (Fabricius 1793) juveniles exposed to a novel and potentially dangerous prey item frequently attack using thrown silk. To quantify the frequency with which *N. clavipes* opt to use thrown silk, naïve hand-reared small *N. clavipes* juvenile females were observed attacking a new prey type, stingless bees. Repeated exposure to the stingless bees suggests that the spiders incorporate prior experience into prey attack strategies, as experienced spiders attacked using the more usual *Nephila* long-bite.

Keywords: *Nephila clavipes*, *Nephila pilipes*, wrap-attack, prey capture, learning

Orb-web building spiders utilize a range of tactics to capture insects that are restrained in the web, and the choice of tactic varies among species and with prey type (Robinson & Mirik 1971; Robinson & Robinson 1976; Eberhard 1982; Japyassú & Viera 2002). One prey-capture tactic, throwing silk with leg IV, is widely used in phylogenetic analyses of the families of entelegyne spiders (e.g., Sharff & Coddington 1997; Griswold et al. 1999; Agnarsson 2004). In these analyses, the family Nephilidae (previously a tetragnathid subfamily Nephilinae; Kuntner 2006) was assumed to lack this behavior and to attack all prey by biting (Robinson & Robinson 1976; Eberhard 1982; Kuntner 2005a, 2006, 2007) which, since the wrap attack is synapomorphic for the orbicularians (Griswold et al. 1999; Agnarsson 2004), made this a secondary loss in the Nephilidae. This character assignment was based upon observations of adult female *Nephila* species. However, failure to observe attacks using thrown silk in diverse web-building spiders may reflect limited studies, either with only mature animals or with prey that are small relative to the spider's size. Here, I report juvenile females of two *Nephila* species attacking with thrown silk. Importantly, the thrown silk attack was only employed by naïve juveniles exposed to a novel insect (*Trigona* stingless bees); spiders with prior experience with bees did not use this behavior.

Differences in experience can have an effect on a variety of spider behaviors, from spatial orientation (salticids, Hoefler & Jakob 2006) to mate choice (Hebets 2003). Prior experience alters predatory behavior in some non-web building spiders (i.e., Salticidae, Edwards & Jackson 1994; Skow & Jakob 2005; and Thomisidae, Morse 2000). Although web-building spiders are often assumed to have less capacity to learn, experiments with various species have shown that prior experience affects web architecture (e.g., Heiling & Herberstein 1999; Nakata & Ushimaru 2004; Prokop 2006), propensity to attack particular prey (Herberstein et al. 1998), and searching behavior when captured insects are removed (Rodriguez & Gamboa 2000). Although the conditions under which spiders are stimulated to attack via thrown silk have been studied for several species of Araneidae (Robinson 1975; Robinson & Robinson 1976), there are no published records indicating a role of prior experience in capture tactics used by orb-weaving spiders. Rather, researchers have concluded that the sequence of attack behaviors is a direct response to the prey type and size and the success or failure of a given tactic *during* an attack (Robinson & Mirick 1971; Robinson et al. 1971; Robinson & Robinson 1976; Herberstein et al. 1998; Japyassú & Viera 2002). However, these experiments involved only adult females, and juveniles may exhibit learning as they gain experience with diverse prey types.

Casual observations of capture by small juvenile *Nephila clavipes* (Linnaeus 1767) (Araneae, Nephilidae) indicated that prior experience can influence how a spider attacks a potentially dangerous prey item (Higgins, unpubl. data). In particular, naïve juveniles frequently threw silk to subdue novel large prey items, a tactic previously reported as absent from the prey-capture repertoire of adult *N. clavipes* (Robinson & Mirick 1971; Robinson 1975; Eberhard 1982). To determine the frequency of this tactic in juveniles interacting with novel prey items, I conducted an experiment with laboratory-reared juvenile *N. clavipes* in Panama and casual observations of field-collected *N. pilipes* (Fabricius 1793) in Papua

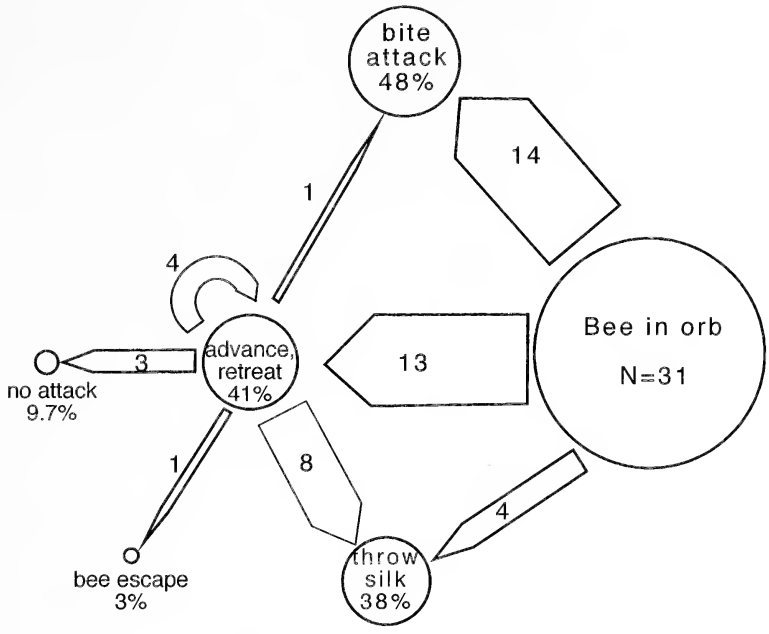

Figure 1.—Behavioral sequences of 31 juvenile *N. clavipes* attacking a *Trigona* bee for the first time. The number in each circle is the percentage of individuals using that behavior (the individuals that repeated "advance, retreat" are only counted once each). The number on each arrow is the number of times that particular transition was observed.

New Guinea (previously *N. maculata,* Kuntner 2005b). Voucher specimens for both species were placed at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

In December 1985, I collected gravid female *N. clavipes* on Barro Colorado Island, Panama (9°N, 80°W) and housed them in an open-air insectary in the laboratory clearing to collect egg sacs. After the emergence of young and their dispersal to individual orb-webs, I placed groups of spiderlings in screen cages in the insectary, and fed them *ad libitum* with fruit flies collected at banana baits. After molting to the fourth instar, about 0.3 cm leg I tibia + patella, I placed haphazardly-selected individual juveniles on 23–25 cm diameter spherical frames (two intersecting circles of 0.25 cm fiberglass strips) hung in the insectary, upon which they spun orb and barrier webs. Juveniles were offered 3 fruit flies daily (total, about 2.7 mg wet weight) until the next molt, after which they measured approximately 0.5 cm leg I tibia + patella length (TPL).

To determine the prey-capture strategies of these juveniles, I offered each of thirty-one fifth-instar spiders a chilled stingless bee (*Trigona* sp., 3.67 mg mean wet weight, approximately 20% of these spiders' body mass and equal to their TPL). These chilled bees rapidly recovered enough to move, but not to fly, within the time frame of these observations. Occasionally, I over-cooled bees: if dead, I vibrated the bee with a tuning-fork until the spider responded. The experienced spiders readily attacked vibrated dead bees, therefore I interpreted refusal of a dead bee by a naïve spider as rejection of the insect because it was a bee rather than because it was dead. I recorded each individual's response to the bee until the prey was either definitely rejected (after approaching the bee and retreating, the spider remained at the hub > 5 min) or captured and removed to the hub of the web. Chilled bees and dead, vibrated bees are grouped in these analyses due to small sample sizes.

Robinson & Mirick (1971) provide descriptions of adult *Nephila* attack behavior, which I here modify to reflect observed juvenile behaviors. A "bite attack" is an approach followed immediately by a direct bite that is sustained. "Advance and retreat" is an approach followed by retreating to the hub of the web. During a "thrown-silk attack," the spider approached the bee, turned around, and placed silk over the insect using the fourth pair of legs.

The juvenile spiders responded variably to the bees (Fig. 1). The sample size was not sufficient to test for small effects of spider weight or days since molting (age within instar). Of the 27 successful attacks on *Trigona* bees, 15 spiders used the typical *Nephila* long bite attack (one after advance and retreat), followed by pulling the bee from the orb, wrapping it and returning it to the hub suspended from a silk thread. Four spiders immediately attacked the bee using thrown silk followed by a bite, a "wrap-bite"

couplet. Many spiders (13) advanced and retreated from the bee. These approaches involved touching the bee, and may have involved attempted bites. Three of these spiders, after one or more approaches, never attacked; one spider approached the bee three times without attacking. On one occasion the bee escaped after the spider had approached and retreated. Of the successful attacks following exploratory approaches, one spider used a bite attack and eight spiders threw silk. Usually, no clear bite was observed until after the spider had removed the wrapped bee to the hub.

I only observed the exploratory approach and subsequent use of thrown silk in naïve spiders. When I repeated the offering of bees to these juveniles, all switched tactics to the long bite attack by the second or, rarely, the third feeding. This behavioral flexibility is distinct from the behavioral sequence plasticity reported for *Nephilengys* by Japyassú & Viera (2002), where mature females altered the attack sequence *during* attacks, but were not *sequentially* tested for shifts in attack strategy.

A thrown-silk attack was seen once in the field in Panama. In this case, a mature female *N. clavipes* (1.2 cm leg I tibia + patella length, approximately 2 cm body length) wrapped but did not bite an approximately 10 mm hemipteran bug. Over a period of 1.5 h, she repeatedly placed silk over the bug using leg IV, capturing it between the thrown silk and the orb-web mesh, and the bug continued struggling and freeing itself. The spider was not observed to bite the bug, and it eventually escaped.

At the Christensen Research Institute (now closed) in Madang, Papua New Guinea (5°13′S, 145°48′E), I recorded attack strategies for sixteen fourth-instar juvenile *N. pilipes* in an insectary during an experiment on developmental plasticity (Higgins 1995). These spiders are the same size as the *N. clavipes* juveniles used in the above-described experiment. All of these individuals were assigned to receive either one or two wild-caught *Trigona* bees daily. I recorded the attack sequence used by these juveniles for the first two bees that were provided. The attack sequences were highly variable, involving six different responses: advance and retreat, touch, long bite, short bite, wrap attack, and cut-silk attack, and were often very long with repeated couplets such as "wrap and bite," "touch and bite," and "touch and wrap." Only 9 (56.25%) of the first attacks were successful; two individuals threw the bee away after subduing it, and five allowed the bee to escape. One individual did not successfully capture a bee until the fourth attempt. *Nephila pilipes* juveniles exhibited one novel attack mode not seen in *N. clavipes*. Eleven (68.75%) of the spiders at some point during their attack cut the orb above or beside the bee so that it collapsed over the insect; two individuals cut the silk as an initial response. Ten (62.5%) of the spiders used thrown silk to attack the prey at some point during the attack (often following short bites or cut-silk attacks). All of the successful attacks included thrown silk at some point of the sequence, and 6 of the successful attacks included cutting the orb. In all cases, attacks on bees after a successful attack were greatly simplified and usually involved just biting, pulling, and returning to the hub (with or without wrapping after removing the bee from the orb).

The exploratory approaches and the thrown-silk and cut-silk attacks are distinct from adult *Nephila* attack behaviors (Robinson & Mirick 1971). "Bite-and-back-off" attacks by adults involve retreating only short distances from the prey, whereas these juveniles retreated to the hub of the orb (16–25 cm radius orb-webs), and often the bee was healthy enough to escape. In addition, the observed thrown-silk attack behavior differs from *in situ* wrapping reported for adult females. Robinson & Mirick (1971) describe *in situ* wrapping by adult female *N. clavipes* as occurring only after the spider has bitten and attempted to pull the prey free of the web; in fact, they experimentally elicited this behavior by restraining prey when the spiders attempted to pull it free. The juveniles I observed were capable of pulling the bee free and wrapping; in *N. clavipes*, all direct bite attacks were followed by this behavioral sequence. None of the juveniles that threw silk attempted to pull the bee free before using this tactic.

The thrown-silk attack by *Nephila* greatly resembles the wrap-attack of araneoid spiders. After approaching, the *Nephila* juveniles turned away from the prey and threw silk using legs IV. Unlike wrap-attacks, the bees did not rotate but became sandwiched between the silk mat thrown by the spider and the fine mesh of the orb. The spider would then cut the bee free of the orb, attach a silk thread, and carry it to the hub hanging from this thread. Biting followed the return to the hub. The main difference between the *Nephila* thrown-silk attack and the araneoid attack wrap is the failure of *Nephila* juveniles to rotate the prey "rotisserie-style" around a radius or several viscid spiral strands between two radii (Eberhard 1967). This difference may reflect physical constraints imposed by the extremely fine mesh of the juvenile *Nephila* orb web. With a body length of 0.4–0.6 cm, *Trigona* bees are larger than the 0.1 cm orb mesh of *Nephila* juveniles (Higgins & Buskirk 1992).

It is widely reported that *Nephila* spiders lack the "attack-wrap" or "wrap and bite" behavior that other orb-web spiders use to deal with large or potentially dangerous prey (Robinson & Mirick 1971; Robinson et al. 1971; Robinson 1975; Eberhard 1982; Kuntner 2005b, 2006). Most recent studies have focused on adult females, to standardize the assessment of this character for phylogenetic analyses (Kuntner pers. com.). The use of a thrown-silk attack by juvenile *N. clavipes* and *N. pilipes* is

correlated with each individual's experience with these relatively large insects. *Trigona* bees are potentially dangerous prey for small *N. clavipes* and I have observed them kill juveniles in Panama. The observation of an adult female *N. clavipes* using this attack against a bug, perhaps chemically defended, indicates that the behavior is not lost with maturation. It is possible that the rarity of the thrown-silk attack is due to the large size of mature females and the relatively small size of the common prey items (Rypstra 1981; Nentwig 1985; Higgins 1987; Higgins & Buskirk 1991). Future studies should address why this tactic is so rarely employed and whether the observed differences with the classic wrap-attack behavior simply reflect a physical constraint due to the fine structure of the *Nephila* orb web.

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SHORT COMMUNICATION

ON SOME CHILEAN JUMPING SPIDER TYPE SPECIMENS DESCRIBED BY NICOLET (ARANEAE, SALTICIDAE)

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ABSTRACT. The type specimens of ten of Nicolet's species of jumping spider from Chile were examined. In this paper we present seven new synonymies and two new combinations for these nominal species as well as a redescription and illustrations where necessary. *Attus iricolor* Nicolet 1849, *Attus scalaris* Nicolet 1849, *Attus superbus* Nicolet 1849 and *Attus zonarius* Nicolet 1849 are synonymized with *Dendryphantes mordax* (C.L. Koch 1846); *Euophrys quilpuensis* Simon 1901, *Attus vanus* Nicolet 1849 and *Attus vestitus* Nicolet 1849 are synonymized with *Euophrys rusticana* (Nicolet 1849) comb. nov.; *Attus legibilis* Nicolet 1849 is tentatively transfered to *Dendryphantes* C.L. Koch 1837.

Keywords: Chile, South America, taxonomy, *Dendryphantes*, *Euophrys*

The earliest publication dealing with Chilean arachnids was by Nicolet (1849), who described several new species of spiders including 29 species of Salticidae. The original descriptions, however, are insufficiently detailed to allow for the accurate identification of the species. Nicolet's entire collection was lost amongst the Muséum National d'Histoire Naturelle, Paris, collection and all have long been treated as *nomina dubia* (Roewer 1955).

After many years treated as lost, 12 of the 29 Nicolet salticid types were located by Ramírez (1989) in the Paris collection. After examining some of these specimens, Galiano (1995) synonymized *Attus similis* Nicolet 1849 with *Attus notabilitatus* Nicolet 1849, redescribing and transferring the species during the description of *Trydarssus* Galiano 1995. The other ten species, however, are still treated as *species inquirendae* (Platnick 2006).

Recently, Christine Rollard and Elise-Anne Leguin kindly sent us the type material of ten of the species located by Ramírez (1989), including those already examined by Galiano (1995). In this paper we present seven new synonymies and two new combinations for these nominal species as well as a redescription and illustrations where necessary. The type specimens of the two other species located by Ramírez have not been examined: the types of *Attus elegans* Nicolet 1849 are on loan to another researcher and those of *Attus modestus* Nicolet 1849 could not be found in the collection by the curatorial staff. The former species, *Attus elegans* Nicolet presently *Thiodina nicoleti* Roewer 1951, was revised by Simon (1900) and designated as the type species of *Thiodina* Simon 1900.

The material examined for this study is deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN). The abbreviation MNHU is used for the Museum für Naturkunde der Humboldt-Universität, Berlin. Measurements are in mm. The following abbreviations were used in the spination formulae: d = dorsal; p = prolateral; r = retrolateral; v = ventral; di = distal.

TAXONOMY

Family Salticidae Blackwall 1841
Genus *Dendryphantes* C.L. Koch 1837

Type species.—*Araneus hastatus* Clerck 1757.

Remarks.—True species of *Dendryphantes* are holarctic in distribution, with only one species in the northern nearctic (Maddison 1996: 236). The Chilean species examined in this study are placed in this genus, but probably do not belong there. Their placement should be considered tentative. The neotropical dendryphantines are in need of much revisionary work.

Dendryphantes mordax (C.L. Koch 1846)

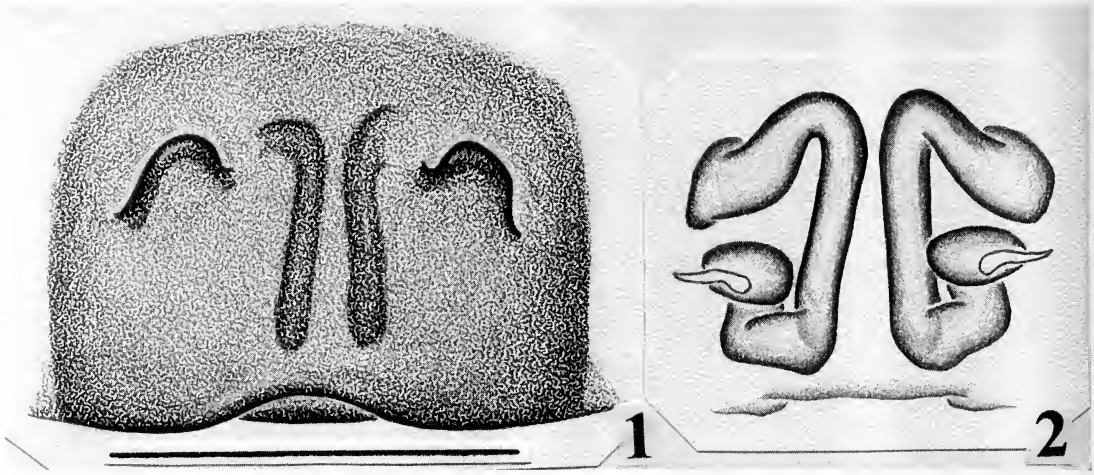
Hyllus mordax C.L. Koch 1846:165, fig. 1219.

Euophrys jucunda C.L. Koch 1846:205, fig. 1252 (synonymized by Galiano 1979: 342).

Attus iricolor Nicolet 1849:366. NEW SYNONYMY.

Attus scalaris Nicolet 1849:365. NEW SYNONYMY.

Attus superbus Nicolet 1849:380. NEW SYNONYMY.



Figures 1–2.—*Dendryphantes legibilis* (Nicolet, 1849). 1. Epigynum, ventral view; 2. Epigynum, dorsal view, cleared. Scale line = 0.25 mm.

Attus zonarius Nicolet 1849:373. NEW SYNONYMY.

Freya jucunda: C.L. Koch 1850:66.

Dendryphantes mordax: Simon 1901a:601; Galiano 1979:342, figs. 1–6; Platnick 2006.

Phiale jucunda: Simon 1903:702.

Type specimens.—*Hyllus mordax:* URUGUAY: male holotype, Montevideo [34°51′S, 56°10′W] (MNHU), not examined.

Euophrys jucunda: URUGUAY: female holotype, Montevideo [34°51′S, 56°10′W] (MNHU), not examined.

Attus iricolor: CHILE: juvenile holotype, Santiago [33°27′S, 70°40′W], C. Gay (MNHN 4149), examined.

Attus scalaris: CHILE: 4 male and 4 female syntypes, Santiago [33°27′S, 70°40′W], C. Gay (MNHN 4167), examined.

Attus superbus: CHILE: female holotype, Valdivia [?] (MNHN 4172), examined.

Attus zonarius: CHILE: 1 male and 1 female syntypes, Santiago [33°27′S, 70°40′W], C. Gay (MNHN 4166), examined.

Description.—See Galiano (1979).

Remarks.—The synonymies are based on the excellent illustrations provided by Galiano (1979, figs. 1–6). The immature holotype of *Attus iricolor* was identified by the general body shape. *Dendryphantes mordax* is known from Uruguay, Argentina and Chile (Platnick 2006).

Dendryphantes legibilis (Nicolet 1849)
new combination
Figs. 1, 2

Attus legibilis Nicolet 1849:366.

Type specimen.—CHILE: female holotype, no further locality data (MNHN 4186), examined.

Description.—*Female:* Total length: 6.05. Color pattern poorly preserved. Carapace light brown, 2.45 long, 1.82 wide, 1.07 high. Ocular quadrangle 1.10 long. Anterior eye row 1.35 wide, posterior 1.60 wide. Chelicerae yellow, with two teeth on promargin and one on retromargin. Palpi yellow, with a femoral spine d1di. Sternum yellow. Leg I light brown, II–IV yellow. Length of femur I 1.30, II 1.05, III 1.05, IV 1.30; patella + tibia I 1.80, II 1.25, III 1.20, IV 1.55; metatarsus + tarsus I 1.07, II 0.90, III 1.00, IV 1.22. Leg spination: femur I, II d1-1-1, p2di; III d1-1-1, p2di, r1di; IV d1-1-1, p1di or p0, r1di; patella I, II, III, IV 0; tibia I v2-2-2; II v1r-2; III v2di or v1pdi; IV v1p-2; metatarsus I, II v2-2; III p1di, r1di, v2di; IV p1di, r1di, v1p-2. Abdomen yellow. Epigynal plate rectangular, invaginated posteriorly; internally with long and coiled copulation ducts and small, oval spermathecae (Figs. 1, 2). Spinnerets yellow.

Remarks.—The species is tentatively transfered to *Dendryphantes*, and is known only from Chile (Platnick 2006).

Genus *Euophrys* C.L. Koch 1834

Type species.—*Aranea frontalis* Walckenaer 1802.

Remarks.—The boundaries among euophryine genera are difficult to assess and in need of review. The neotropical species of this genus may not belong to the same lineage as the palaearctic type species.

Euophrys rusticana (Nicolet 1849) new combination

Attus rusticanus Nicolet 1849:374.

Attus vanus Nicolet 1849:379. NEW SYNONYMY.

Attus vestitus Nicolet 1849:379. NEW SYNONYMY.

Euophrys quilpuensis Simon 1901b:21; Berland 1924 437, figs. 38–41; Galiano 1962:177, pl. I, figs. 8–14; Galiano 1963:352, pl. XIX, fig. 5; Prószyński 1976:153, figs. 174, 215; Platnick 2006. NEW SYNONYMY.

Type specimens.—*Attus rusticanus:* CHILE: 5 female syntypes (MNHN 4165), examined.

Attus vanus: CHILE: 2 male syntypes, Valdivia [?], C. Gay (MNHN 4185), examined.

Attus vestitus: CHILE: 5 male syntypes, Valdivia [?] (MNHN 4134), examined.

Euophrys quilpuensis: CHILE: female holotype, Quilpué [33°02′S, 71°26′W] (MNHN), not examined.

Description.—See Galiano 1962:177, pl. I, figs. 8–14.

Synonymies.—The synonymy of *Euophrys quilpuensis* Simon 1901b is based on illustrations by Galiano (1962). *Euophrys rusticana* is known only from Chile (Platnick 2006).

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We wish to thank Christine Rollard and Elise-Anne Leguin for sending the specimens and G.B. Edwards for his suggestions on the manuscript. We also thank the "Conselho Nacional de Desenvolvimento Científico e Tecnológico" (CNPq) for financial support.

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2007 (2008). The Journal of Arachnology 35:538–542

SHORT COMMUNICATION

A PROTOCOL FOR DIGESTING INTERNAL SOFT TISSUES AND MOUNTING SPIDERS FOR SCANNING ELECTRON MICROSCOPY

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ABSTRACT. We describe a simple protocol for digesting the internal soft tissues of spiders using an enzyme complex known as pancreatin. This technique is preferred over digestions with caustic agents because it better preserves the cuticle surface, allowing its study by means of scanning electron or transmitted light microscopy. In addition, we describe a technique for mounting spider body parts for scanning electron microscopy using an acryloid polymer.

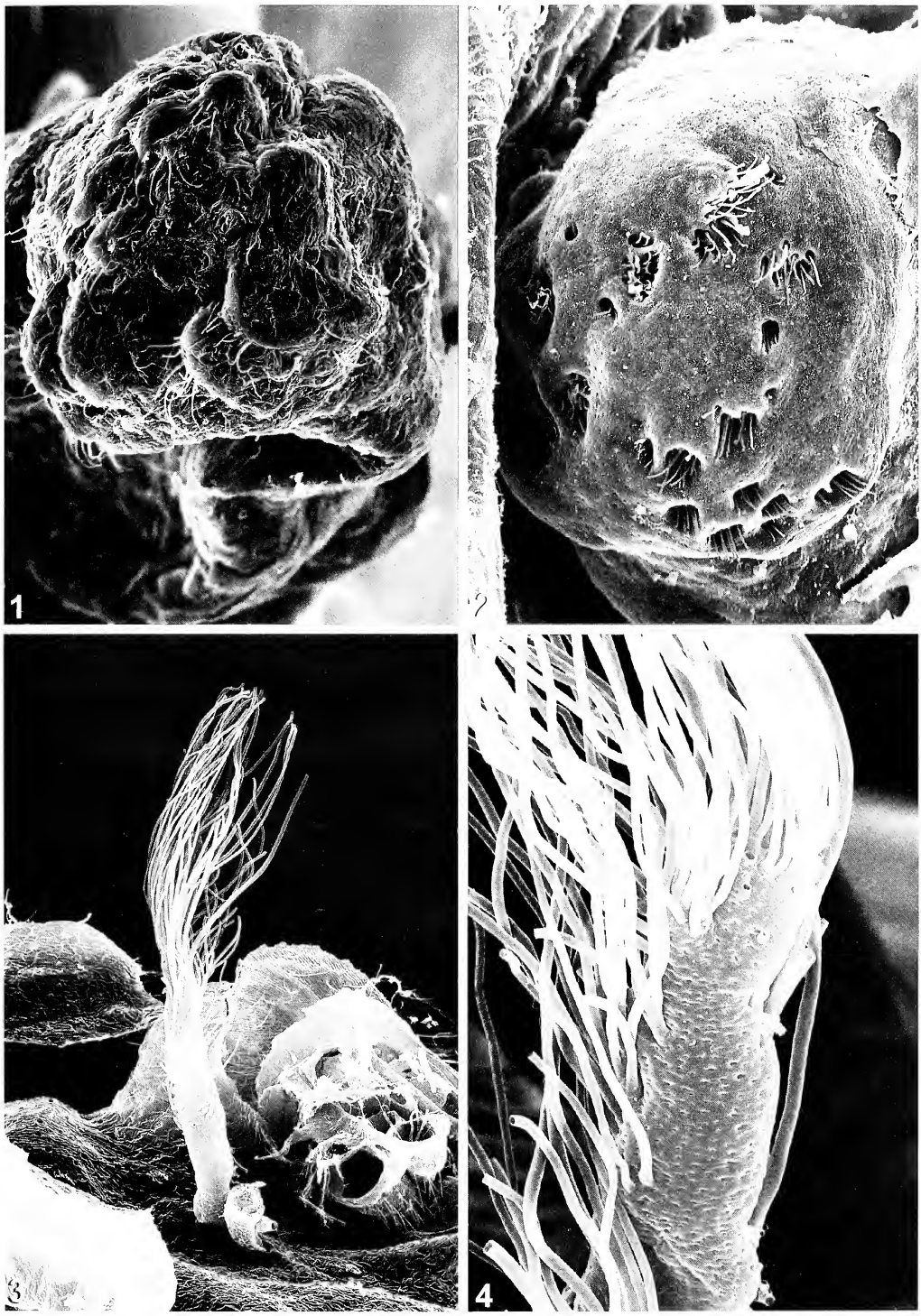
Keywords: Digestion, pancreatin, dissection, SEM

Protocols for digesting internal soft tissues have been widely used in the entomological and arachnological literature either to observe the morphology of internal structures (e.g., Purcell 1909, 1910; Lamy 1902; Machado 1951; Millidge 1984; Wibel et al. 1984; Meyer 1989; Sierwald 1989; Platnick et al. 1999; Ramírez 2000; Townsend et al. 2000; Griswold et al. 2005) or to estimate the proportion of skeletal tissues in insects (Buxton 1932). Potassium hydroxide (KOH), sodium hydroxide (NaOH) and sodium hypochlorite (NaClO, bleach) are some of the most commonly used substances in these studies. The purpose of such digestions is to remove the soft tissues that surround sclerotized organs for study with scanning electron microscopy (SEM) or optical microscopy. Digestions with the above mentioned chemical agents can damage the chitinous cuticle surface of structures such as spermathecae, therefore the use of less aggressive substances, such as trypsin, has been recommended (e.g., Sierwald 1989).

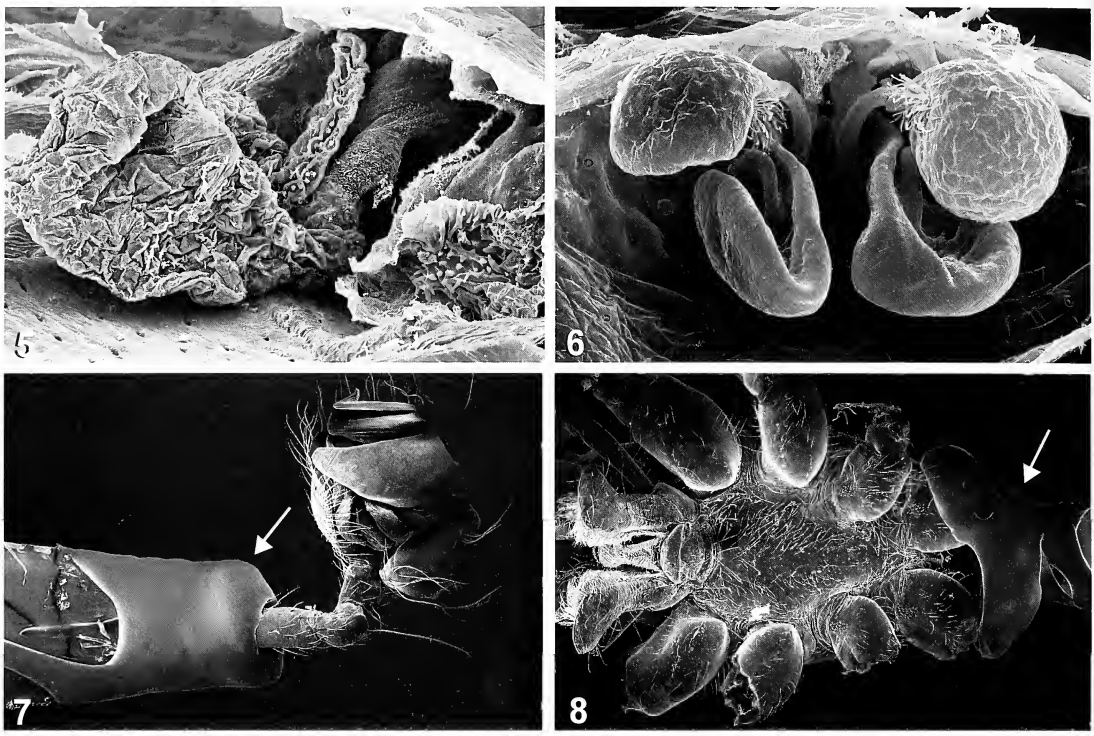
We describe a protocol for digesting spider internal soft tissues with a mixture of digestive enzymes usually obtained from pig pancreas known as pancreatin. Pancreatin contains trypsin, amylases, lipases, ribonucleases, and proteases. Furthermore, this enzyme complex is active at room temperature and does not require buffers. These enzymes effectively digest the soft tissues without apparent damage to the cuticle surface of sclerotized organs (compare Figs. 1 and 2). We have successfully used pancreatin to study the female internal genitalic structures as well as the tracheal system anatomy of a diversity of spider species (e.g., Figs. 3–8; Álvarez-Padilla & Hormiga unpublished ms.). Furthermore, digestion of soft tissues with pancreatin greatly facilitates the microscopic observation of sclerotized structures in clearing media (e.g., methyl salicylate, see Holm (1979)), such as spermathecae and accessory ducts.

Examination of entomological or arachnological specimens for scanning electron microscope (SEM) is commonly done by attaching the specimen (or body part) directly onto the mounting stub or by attaching it to the free end of a piece of wire, usually made of gold or copper. Conductive and non-conductive adhesives are available to glue the specimen to the mount. We have used non-conductive acryloid glue, which has the desired characteristic of producing thin threads. These threads are used to wrap the specimen at the free end of the copper tape. This modification allows us to securely glue the specimen to the copper tape by a small area maximizing the observable surface of the specimen (Figs. 2C, D, arrows). In principle, any glue that forms thin elastic threads and dries out relatively fast can be used for this purpose, but an acryloid B-72 solution in acetone has the advantage that its viscosity can be easily modified by changing the proportion of acetone to acryloid in the mixture. If the acryloid pellets are diluted with too much acetone the solution will not form threads or the threads will break easily. Conversely, too little acetone will result in an unworkable mix of high viscosity. The acryloid B-72 glue is easier to manipulate than the standard graphite conductive glue used for SEM, and once it is covered with gold during the sputter coating process the glue surface becomes conductive although sometimes it may present charging problems.

Pancreatin protocol.—Method is modified after Dingerkus & Uhler (1977). Add sodium tetraborate decahydrate (Borax) to one liter of warm distilled water (60° C) until saturation is reached then cool to room temperature (RT ≈ 20° C). (When the solution cools, a layer of borax crystals will form at the



Figures 1–4.—1. Spermatheca of *Chrysometa alajuela* Levi 1986 (Tetragnathidae) digested with KOH; 2. Spermatheca of *C. alajuela* digested with pancreatin; 3. *Glenognatha foxi* (McCook 1894) (Tetragnathidae) tracheal system digested with pancreatin (left tracheal trunk); 4. Detail of the left tracheal trunk and tracheoles of *G. foxi*.



Figures 5–8.—5. Spermathecae of *Leucauge venusta* (Walckenaer 1842) (Tetragnathidae) digested with pancreatin; 6. Spermathecae of *Nanometa* sp. (Tetragnathidae) digested with pancreatin; 7. Left male pedipalp of *Chrysometa alajuela* (Tetragnathidae), mesal view (arrow indicates acryloid glue thread on copper tape); 8. Cephalothorax of *Tetragnatha versicolor* Walckenaer 1842, ventral view (arrow indicates dried acryloid glue thread around coxa IV on tip of copper tape).

bottom.) Dissolve 1 g of pancreatin 4× USP grade enzyme complex in 70 ml of distilled water, add 30 ml of borax saturated aqueous solution and mix well. Filter the solution with cotton and a funnel to remove the coagulated proteins. Distribute the solution into several vials and keep them frozen (−20° C). The solution can be thawed and frozen several times, and it will work for 3 da at RT.

To enable the pancreatin solution to contact internal tissues a wide opening must be made in the abdomen (e.g., Platnick et al. 1999); or a large section of the specimen must be removed to allow the pancreatin solution to enter (e.g., cut a large window on the dorsal cuticle of the abdomen). For specimens preserved in ethanol, transfer the specimens to a vial with distilled water for one to two hours or until they sink; then transfer the samples to the pancreatin solution.

Specimens $\leq$ 5 mm^3 will take overnight to digest completely. Smaller samples, such as epigyna, will take 4–5 h but can be left overnight too. Samples left $>$ 16 h can be completely digested and destroyed. Digestion times for specimens $\geq$ 5 mm^3 will be $\sim$ 1–3 da. Incubating the samples at $\sim$ 37° C will reduce digestion times. All samples must be cleaned after 24 h of digestion. The cleaning process must be done carefully to avoid damaging the internal sclerotized structures. Transfer the sample to distilled water and remove the partially digested tissue with streams of water produced by a pipette. Return the sample to the pancreatin solution until digestion is completed. Transfer the specimen to 75% alcohol (= ethanol) and wash it with a pipette until the tissue is completely removed. If some soft tissues remain undigested, repeat the transfer to distilled water and then to the pancreatin solution. Once the soft tissues have been digested, transfer the specimens to clean 75% alcohol.

For inspection with a compound microscope transfer the specimens to clove oil, methyl salicylate or some other clearing substance. Temporary slide-mounts for these preparations are described elsewhere (e.g., Grandjean 1949; Coddington 1983). KOH digestions work fine for study with stereo or transmitted light microscopy. However, the cuticle surface may have been over digested by the caustic process making this type of specimen unsuitable for SEM. For SEM study follow standard protocols for critical point drying and sputter coating of the specimen.

SEM mounting protocol.—Dissolve Acryloid B-72 (Paraloid B-72) pellets in acetone until they form a gluey homogenous mix. The viscosity of the mixture can be adjusted by adding or evaporating acetone. The mix should be such that it will produce a thin thread when a needle touches its surface and is then pulled about one centimeter away. If the preparation of the acryloid solution produces many air bubbles (as a consequence of stirring the pellets in acetone), sonicate the vial until all the bubbles have risen to the surface. Unused acryloid solution can be stored in a closed vial and its viscosity readjusted with acetone when needed. Any glue that forms thin elastic threads and dries out relatively fast could be potentially used, but we only have experience with Acryloid B-72.

Take the critically point dried specimen with a fine brush or soft forceps; conventional forceps will easily damage the specimen. Place the specimen (e.g., cephalothorax, pedipalp, leg, etc.) on the free end of the sticky copper tape (the other end of the tape has been attached to the SEM mount). At this point avoid moving the copper tape because this action may easily catapult the specimen. To permanently attach the specimen to the copper tape, collect enough glue with the tip of a needle mounted on a handle (or a thin and straight piece of metal wire), touch the base of the mount with the glue-loaded needle tip and pull the needle until a thin thread of glue is formed. Wrap the specimen and the copper tape with this glue thread several times by going around the area in a circular motion. Once the glue has dried, examine the mounted specimen with the stereoscope at high magnification. If any dirt is visible on the specimen, try to remove it by gently blowing air with a thin glass pipette connected to surgical latex tubing or with the help of a needle or brush. Carefully bend the tip of copper tape with the mounted specimen to the desired orientation. Proceed to sputter coating the preparation.

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Ichthyologists John Burns and Robert Javonillo (The George Washington University) suggested the use of pancreatin for enzymatic digestion of soft tissues. Martin J. Ramírez (Museo Argentino de Ciencias Naturales, Buenos Aires) first recommended the use of copper sticky tape for SEM mounts. Martin J. Ramírez, Diana Silva, Lara Lopardo, Dimitar Dimitrov, Suresh Benjamin, Anahita Shaya, Vanessa Degrassi, John Burns, and Robert Javonillo provided extremely useful comments on an earlier draft of this manuscript. Support for this work has been provided by a NSF-PEET grant to Gustavo Hormiga and Gonzalo Giribet (DEB-0328644), a George Washington University REF grant, and a doctoral scholarship form CONACYT (Mexico) to the senior author.

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SHORT COMMUNICATION

A DESCRIPTION OF THE FEMALE WOLF SPIDER *CAMPTOCOSA TEXANA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. The female of *Camptocosa texana* Dondale, Jiménez & Nieto 2005 is described from Arizona. Females of *C. texana* are compared to those of *C. parallela* (Banks 1898), which differ from *C. texana* females in the color morphology of the carapace and the shape of the median septum.

Keywords: *Camptocosa parallela*, species description

Dondale et al. (2005) created the genus *Camptocosa* and, in doing so, alleviated the problematic placement of the type species *Camptocosa parallela* (Banks 1898) that had been placed in both *Schizocosa* Chamberlin 1904 (Gertsch & Davis 1940) and *Allocosa* Banks 1900 (Roewer 1955). While the male of *C. texana* was described by Dondale et al. (2005), the female was unknown at the time. While examining specimens from Cochise County, Arizona, we discovered male *C. texana* with conspecific females. We present the first description of the female of *C. texana* and compare it with the female of *C. parallela*.

Specimens examined or mentioned in this paper are deposited at the American Museum of Natural History, New York, USA (AMNH) and the Denver Museum of Nature & Science, Denver, Colorado, USA (DMNS).

TAXONOMY

Family Lycosidae Sundevall 1833
Subfamily Lycosinae Sundevall 1833
Genus *Camptocosa* Dondale, Jiménez & Nieto 2005
Camptocosa texana Dondale, Jiménez & Nieto 2005

Camptocosa texana Dondale, Jiménez & Nieto 2005:42, fig. 4.

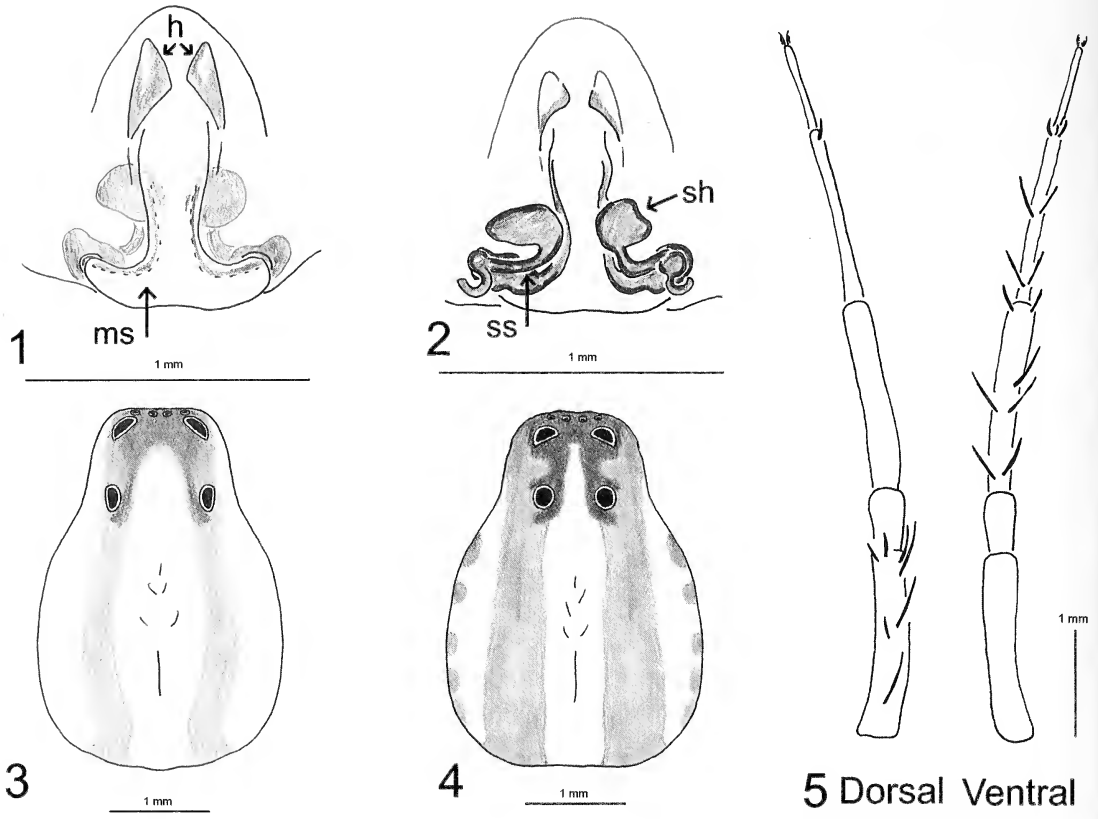
Figs. 1–3, 5

Type material.—USA: *Texas*: Holotype male, 2 miles S. of Riviera, Kleberg County (27.2833°N, 97.8000°W), 14 April 1963, W.J. Gertsch and W. Ivie (AMNH), not examined; 1 paratype male, Hully Gully Cave, Culberson County, 8 July 1970, J. Reddell (AMNH), not examined.

Material examined.—USA: *Arizona*: Cochise County: 1 ♂, Grey Hawk Nature Center (31.6123°N, 110.1654°W), May 2005 (DMNS); 1 ♂, same locale, June 2005 (DMNS); 1 ♂, same locale, August 2005 (DMNS); 1 ♀, Grey Hawk Nature Center (31.6121°N, 110.1650°W), September 2005 (DMNS); 1 ♀, Hereford Bridge (31.5194°N, 110.1295°W), August 2005 (DMNS); 1 ♂, Hereford Bridge (31.5209°, 110.12932°W) (DMNS); 6 ♂, 2♀, San Pedro House (31.5547°N, 110.1384°W), May 2005 (DMNS); 4 ♂, 5 ♀, same locale, June 2005 (DMNS); 1 ♂, 1 ♀, same locale, July 2005 (DMNS); 1 ♀, same locale, September 2005 (DMNS); 1 ♀, same locale, October 2005 (DMNS); 10 ♂, 9 ♀, San Pedro House (31.5562°N, 110.1390°W), May 2005 (DMNS); 2 ♂, 2 ♀, same locale, June 2005 (DMNS).

Diagnosis.—Female *C. texana* can be separated from *C. parallela* by the shape of the epigynum, with *C. texana* having a longer inverted T-shaped median septum with two hoods (Fig. 1), as well as small globular spermathecae (Fig. 2). *Camptocosa texana* has narrower longitudinal bands on the carapace (Fig. 3) and lacks the 5 spots present along the lateral edge of the carapace seen on *C. parallela* (Fig. 4). The legs of *C. texana* are concolorus whereas the legs of *C. parallela* are banded, with legs III and IV having the heaviest bands. The epigynum and spermathecae of *C. parallela* is illustrated in Dondale et al. (2005, figs. 2 & 3) as are the pedipalps of both species (Dondale et al. 2005, figs. 1 & 4); male differences are also outlined by Dondale et al. (2005).

Description.—*Females (n = 5)*: Total length: 6.4 ± 0.51 mm, carapace length: 3.1 ± 0.27 mm, carapace width: 2.4 ± 0.17 mm. Carapace yellow to orange with paired darker longitudinal bands originating from the anterior eye row and extending through the posterior eye row to the posterior end of the carapace (Fig. 3). Bands covered with dark hairs, which may be shed in alcohol. Eye area dark with long white setae present, anterior eye row narrower than posterior median eye row. Chelicerae orange



Figures 1–5.—Female *Camptocosa*. 1–3. *C. texana*, from Hereford Bridge, Cochise County, Arizona: 1. Ventral view of epigynum; 2. Dorsal view of epigynum; 3. Dorsal view of carapace. 4. Dorsal view of carapace of *C. parallela* from Hereford Bridge; 5. Chaetotaxy of leg I of *C. texana* from same locale. Abbreviations: h, hood; ms, median septum; ss, spermathecal stalk; sh, spermathecal head.

with a dusky line longitudinally originating at the boss. Three promarginal teeth, usually represented by one small and one large tooth adjacent to one another and one small tooth separated. Three equally sized retromarginal teeth. Sternum yellow. Abdominal pattern variable, with indistinct heartmark and several dusky chevron-like marks. Venter yellow. Leg formula: 4-1-2-3. Carapace length/leg I length: 0.03. Legs concolorous, yellow to pale orange. Chaetotaxy of leg I: femur, seven (six) dorsal, occasionally macrosetae missing on the median dorsoprolateral position, four located on the distal end; tibia, seven ventral in two pairs, one single, and one distal pair; metatarsus, one dorsal on distal end, six ventral in three pairs (Fig. 5). Epigynum with double hood; prominent median septum in the shape of an inverted T, septum as long as width of base, ends of base end in pockets (Fig. 1). Spermathecal stalk extending mesially from the septal pocket, then turning anteriorly and connecting to a globular or oblong spermathecal head (Fig. 2). Fertilization tube originating from septal pocket area.

Natural history.—Adult specimens of *C. texana* were collected from Cochise County, Arizona throughout May–October using pitfall traps. The highest numbers of spiders were collected from May to June; all were collected in a cottonwood/willow habitat. Specimens of *C. texana* were collected in close proximity to specimens of *C. parallela*; however, no *C. parallela* were collected from the cottonwood/willow habitat.

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SHORT COMMUNICATION

BIOLOGY OF *GALEODES CASPIUS SUBFUSCUS* (SOLIFUGAE, GALEODIDAE)

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ABSTRACT. This study reports on some observations on the biology of the Central Asian solifuge, *Galeodes caspius subfuscus* Birula 1937. Solifuges were active only during summer months. At other times, they were found in burrows located in sandy soils on southeast facing slopes. They were strictly nocturnal in their activity patterns. Small specimens (juveniles) were observed to forage only in the bush using a "sit-and-wait" strategy, while large specimens (subadults and adults) foraged actively only upon the ground. Their prey included various insects including Trichoptera, Coleoptera, and Ensifera. Mating behavior appeared aggressive as several females consumed males either before or after copulation. The mating is described in detail. After mating, females deposited eggs in a burrow and guarded them, presumably until hatching.

Keywords: Camel-spiders, activity, habitat preference, prey, mating, sexual cannibalism

Solifuges are one of the most important predators in arid environments (Polis & Cormick 1986). They occur across the world except for Australia (Punzo 1998a). Despite being very abundant, little attention has been paid to their biology or ecology. Extensive work has thus far only been carried out on North American eremobatids (e.g., Muma 1966a, b, 1967; Punzo 1997). European, Asian, African, and South American species have rarely been studied (Cloudsley-Thompson 1961; Junqua 1966; Wharton 1987).

One of the most common species in Central Asia is *Galeodes caspius* Birula 1890 (Galeodidae). It is one of the largest species, attaining a body size up to 7 cm, and has been described in four subspecies (Harvey 2003). Virtually no data on any aspect of their biology has been published so far. Thus, our goal was to elucidate the main aspects of biology of *Galeodes caspius subfuscus* Birula 1937 that occurs in Kazakhstan and Kyrgyzstan. Specifically, we focused on circadian activity, habitat preference, predatory behavior, prey preferences as well as mating and post-mating behavior.

The study areas were slopes and plains (43°57′53″N, 77°03′11″E) along the Illi River in Kapchagay, in the southern part of semi-desert Taukum in southeast Kazakhstan. Observations were made during 2 wk in April and 2 wk in June 2004 and 2005. In April we focused on habitat preference by investigating factors influencing the position of burrows. In June we performed nocturnal observations using UV light in order to observe their foraging activity. Also in June, adult solifuges were collected and the mating behavior was studied in a shelter. A male and a female were put in a plastic box (25 × 15 × 6 cm) after being fed with grasshoppers to satiation. The mating that followed was recorded. Mated females were brought to the laboratory in order to continue our observations on post-mating behavior. Voucher specimens are deposited in the collection of arachnids of the Institute of Botany and Zoology, Masaryk University, Brno, Czech Republic.

Habitat.—Burrows occupied by solifuges were found by turning over stones. For each burrow (n = 60) the diameter and the length of the burrow, size of solifuge, the size of the stone, type of soil, and slope were recorded. The size of the burrow increased significantly with solifuge size (linear regression, $F_{1,50}$ = 132, $P < 0.0001$). The size of stones (area) was independent of solifuge size (linear regression, P = 0.16) as it was on average 488 cm^2 (SE = 55.7). Similarly the thickness of the stone was independent of the solifuge size (linear regression, P = 0.32), it was on average 8 cm (SE = 0.55). The solifuges

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Table 1.—Number of solifuges found as a function of soil type and aspect.

Soil type (n = 3)	Aspect (n = 3)		
	South	South-East	South-West
Loess	12	5	0
Sand	0	28	5
Sandloess	0	10	0

showed significant preference for a certain type of aspect (= compass direction) and soil (contingency tables, $\chi^2_4 = 40$, $P < 0.0001$, Table 1), with the majority of them (72%, $n = 60$) occurring on the SE slope. The remaining ones were found either on S (20%) or SW facing (8.3%) slopes. Many (55%) burrows were found in sandy soils, the rest in the loess and sandy loess.

Solifuges hiding in burrows had been mentioned by several authors (e.g., Cloudsley-Thompson 1977; Punzo 1998b), and solifuges living in deep burrows under stones were observed in some North American species (Muma 1967). The burrows in other *Galeodes* species were found to be up to 240 mm deep (Berland 1932) and plugged by dead leaves (Cloudsley-Thompson 1961). Similar to other solifuges (e.g., Cloudsley-Thompson 1977; Punzo 1998b), *G. caspius subfuscus* individuals use burrows while resting during the day, as a protection during molting, and for the deposition of eggs. These solifuges clearly place burrows on slopes having a southerly aspect where they are exposed to solar radiation. This is particularly important during spring months when temperature, which affects rate of development, is rather low.

Circadian activity.—In April no solifuge was seen moving on the ground either during the day or at night. By June they were active but only at night and we observed dozens of individuals ($n = 125$). Their activity started at 21:00 (sunset) and terminated at 01:00, with maximum activity at 22:00 (Table 2). Most solifuge species are nocturnal (e.g., Lawrence 1955; Punzo 1998b) like other predators in arid environments. However, large species are strictly nocturnal (Cloudsley-Thompson 1977), presumably an adaptation to avoid predators, low humidity, and heat.

Predation.—Foraging behavior of juveniles was different than that of subadult and adult solifuges. Small individuals (juveniles) hunted exclusively on the bushes ($n = 78$) using a "sit-and-wait" strategy, whereas large individuals (subadults and adults) hunted only on the ground ($n = 47$) using active prey chasing. Juvenile solifuges hung from the branches (Fig. 1) with out-stretched pedipalps that grasped flying prey such as Trichoptera. This foraging habit has not been reported for any solifuge so far. Indeed, the majority of solifuges, both juveniles and adults, search for prey on the ground (e.g., Muma 1967).

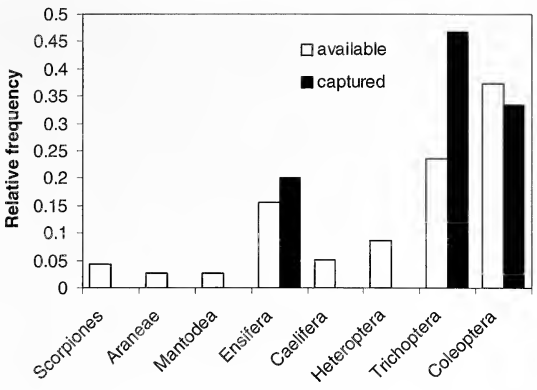

Figure 1.—Comparison of the available and captured prey by juvenile and adult specimens (pooled) of *G. caspius subfuscus*.

We investigated potential (available) prey by recording representatives of insect orders occurring in bushes and on the ground during an hour. The composition of available prey was then compared with the composition of captured prey. *Galeodes caspius subfuscus* captured mainly ($n = 15$) Trichoptera imagoes, Coleoptera larvae, and Ensifera (Fig. 2), which corresponds well to the composition of the available prey (chi-square test, $\chi^2_7 = 7.2$, $P = 0.41$). This also suggests that this solifuge is polyphagous.

Solifuges are reported to be predators with an extraordinary voracity; however, only a few field observations on solifuge foraging behavior have been made (Bolwig 1952; Muma 1966b; Wharton 1987). Apart from a few specialized termite-eating species (for example, *Chelypus hirsti* Hewitt 1915 or *Ammotrechella stimpsoni* Putnam 1883), most solifuges are generalists, feeding mainly on insects (Ensifera and Coleoptera) and arachnids (e.g., Cloudsley-Thompson 1977; Punzo 1997).

Table 2.—Number of individual solifuges active at particular times of the day in June. Hours with no activity are not included.

Hour	20:00–21:00	21:00–22:00	22:00–23:00	23:00–24:00	24:00–1:00
n	1	51	39	29	5

Figure 2.—A juvenile *G. caspius subfuscus* foraging in the bush with outstretched pedipalps.

Mating.—We observed mating behavior in five pairs; in another three pairs, the male was consumed by the female prior to mating. Observed matings lasted on average 3 min 20 s and could be split into several stages. Typically, the male approached the female with raised pedipalps. The female either responded aggressively - raising her pedipalps and trying to attack the male, or became paralyzed after being touched by the male's pedipalps. If the female responded aggressively, the male suddenly fastened himself to her body using suctorial organs (Cushing et al. 2005) on pedipalps, jumped over her body and delivered a bite to the lateral region of her propeltidium. Then he began to chew her propeltidium (Fig. 3), which caused paralysis of the female. He then continued to chew the lateral and ventral parts of her abdomen close to the genital opening. During chewing, he forcibly twisted her abdomen over her propeltidium and started to chew the genital opening. While chewing, he lifted himself on all legs and released an amorphous spermatophore about 5 mm in diameter (Fig. 4). The male then grasped the spermatophore by his chelicerae and pushed it into the genital opening (Fig. 5). Immediately after the insemination, the male departed before the female awoke from the apparent paralysis (Fig. 6). After a successful copulation, males would try to copulate with a new female; however, they were unable to produce a new spermatophore. Mating behavior has been described for only a few species of solifuges so far (e.g., Amitai et al. 1962; Muma 1966a; Wharton 1987; Punzo 1997). As there are large differences between families, our knowledge about the mating of solifuges is incomplete. Within the approaching phase, striking the female with pedipalps appears to be behavior common to solpugids (Wharton 1987) and galeodids (Amitai et al. 1962; Cloudsley-Thompson 1967). It has not been seen in eremobatids (e.g., Punzo 1997). The paralyzing phase has not been observed in eremobatids (Muma 1966a), only in solpugids (Wharton 1987). There are also differences within the family. While in *G. sulfuripes* Roewer 1934 (Amitai et al. 1962) the male used only one chelicera for the insemination, in *G. granti* Pocock 1903 (Cloudsley-Thompson 1961), *Othoes saharae* Panouse 1960 (Junqua 1966), and *G. caspius subfuscus* (this paper) both chelicerae were employed.

In our study, nearly half of the males ($n = 8$) were consumed by the females either prior to or after mating. Similar cannibalism has been observed in other galeodids (e.g., Cloudsley-Thompson 1977), but not in eremobatids (Punzo 1997). We do not know exactly why the cannibalism occurred. After consuming a male, the female was able to mate a second time ($n = 3$). Sexual cannibalism in solifuges is not widely recognized as it is not mentioned in a review of cannibalism (Elgar & Crespi 1992). Our limited observations support the mistaken identity hypothesis (Elgar & Crespi 1992).

Post-mating.—In the field, we found one female guarding an egg clutch within a burrow. In the laboratory, approximately one month after mating, females laid eggs. There were on average 107 eggs in a clutch ($n = 4$). The eggs were whitish in color, spherical in shape and on average 2.8 mm in diameter. Larvae hatched after about 20 days at ~ 23° C. They were immobile and molted to the first free instar after about another 20 days.

The eggs of other solifuge species have similar shape and color to those observed in *G. caspius subfuscus*, but they were different in size and number per clutch as larger species produced larger eggs and masses (Cloudsley-Thompson 1977). *Galeodes granti* laid 32 pearly white eggs 4 mm in diameter (Cloudsley-Thompson 1961). Guarding behavior is not typical for many solifuges. Until now, guarding behavior has been observed in some galeodids (Cloudsley-Thompson 1967), solpugids (Lawrence 1949), and one eremobatid species (Punzo 1998b). Females of other eremobatids and ammotrechids simply plugged and concealed the burrow entrance after the deposition and abandoned the eggs (Muma 1967; Cloudsley-Thompson 1977).

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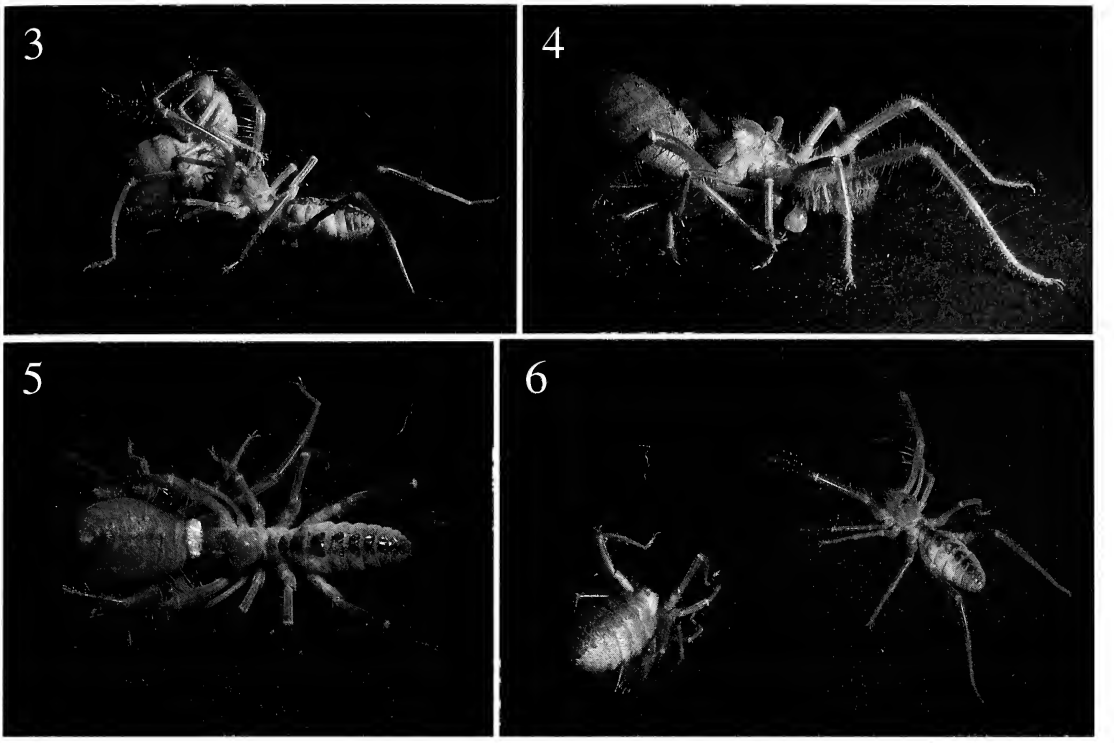

Figures 3–6.—Mating sequence. 3. Male grasping the side of female propeltidium. 4. Male producing the spermatophore while chewing her genital opening. 5. Male inserting spermatophore into genital opening with chelicera. 6. Mating has finished, female is still in paralysis, while male is retreating.

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SHORT COMMUNICATION

THE MIOCENE WHIPSCORPION *THELYPHONUS HADLEYI* IS AN UNIDENTIFIABLE ORGANIC REMAIN

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ABSTRACT. The putative fossil whipscorpion *Thelyphonus hadleyi* Pierce 1945 (Arachnida: Uropygi) from the middle to late Miocene Monterey Formation of Cabrillo Beach, San Pedro, California is reassessed. It is shown here to be nothing more than a fortuitously shaped stain on the rock, apparently partly algal in nature. The fossil record of whipscorpions can thus be restrained to six Pennsylvanian and one Cretaceous species.

Keywords: Uropygi, fossil, taxonomy, Monterey shale, Cabrillo Beach

Whipscorpions (Arachnida, Uropygi) are a distinctive group of arachnids characterized by robust, subraptorial pedipalps, a slender first pair of legs and an opisthosoma ending in a long, flagelliform whip-like telson. The catalogue of Harvey (2003) recognized a single family containing 103 extant species distributed throughout the tropics of Africa, Asia, and the Americas. Various aspects of their biology were summarized by Haupt (2000) and references therein. The fossil record of the group extends back to the Pennsylvanian of North America and Europe and these Coal Measures fossils were recently revised by Tetlie & Dunlop (in press). Six valid species in four genera were recognized. Five of them resolve as a grade, basal to the extant crown-group Thelyphonidae. Specifically, the earliest fossils apparently lack the projecting apophyses seen in modern whip scorpions which give their pedipalps a distinctly more chelate appearance. The sixth Coal Measures species may belong to the stem-group of Schizomida (schizomids), sharing with this group aspects of carapace morphology (Dunlop & Horrocks 1996) and pedipalps that operate in a more vertical rather than horizontal plane. A single Mesozoic whipscorpion has been recorded from the Early Cretaceous Crato Formation of Brazil. Fully modern-looking, with the pedipalpal apophyses defining the crown-group (e.g., Dunlop & Martill 2002, fig. 4b), these fossils can be assigned with some confidence to Thelyphonidae. Indeed their size—the largest carapace is over 30 mm long—and their biogeographical distribution in the Americas suggest a fossil genus closely related to the extant *Mastigoproctus* Pocock 1894.

This leaves only one further fossil whipscorpion in the literature, *Thelyphonus hadleyi* Pierce 1945, described from the mid to late Miocene (between 15 and 10 Ma) Monterey Formation of Cabrillo Beach, San Pedro, California. Listed by Petrunkevitch (1955), Harvey (2003), and Tetlie & Dunlop (unpubl. data), a particular problem is its assignment to *Thelyphonus* Latreille 1802, a genus restricted today to South-East Asia (cf. Harvey 2003). Intuitively, one would expect it to belong to, or be close to, an American genus such as *Mastigoproctus*. Furthermore, the original description is inadequate and contains only a rather unconvincing photograph, which the author (p. 8) stated "...gives better detail than a description can." Here, we restudy the holotype and only known specimen which, in fact, cannot even be identified as an arachnid.

TAXONOMY

incertae sedis fossil

Fig. 1.

Thelyphonus hadleyi Pierce 1945:7–8, plate 5; Petrunkevitch 1955:120; Harvey 2003:73–74.

Material examined.—Holotype and only known specimen of *T. hadleyi*, Natural History Museum of Los Angeles County, holotype number 2504 (a previous number used by Pierce is A6 paleontology records S9008). From the Carbrillo Beach shore at San Pedro, California, USA. Neogene, mid to late Miocene, Monterey Formation. E.E. Hadley, November 1944.

Description.—Total length 20.5 mm; "opisthosoma" ca. 8 mm long with maximum width of

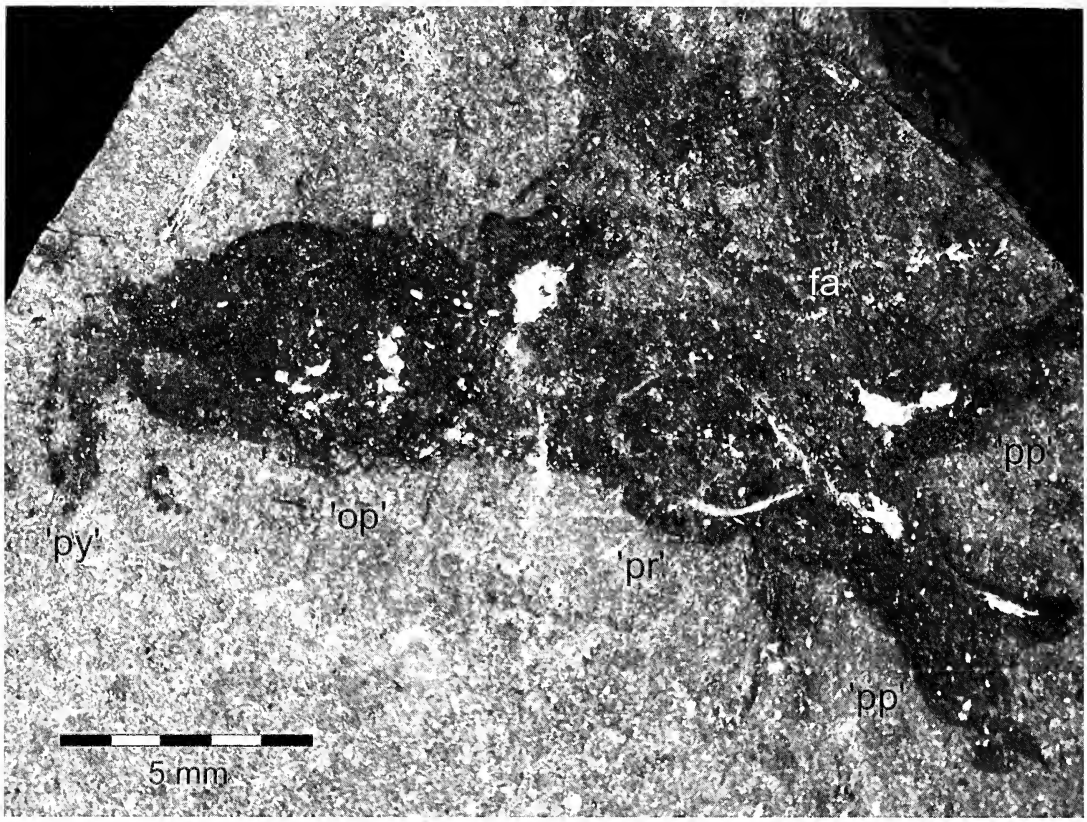

Figure 1.—Holotype and only known specimen of *Thelyphonus hadleyi* Pierce 1945 from the Miocene Monterey Formation of Cabrillo Beach, California. Originally assigned to the whipscorpions (Uropygi), but in fact *incertae sedis* organic remains that cannot be taxonomically assigned. At least some parts of the fossil represent filamentous algae. Abbreviations: fa, filamentous algae; "op," putative opisthosoma; "pp," putative pedipalps; "pr," putative prosoma; "py," putative pygidium.

4.5 mm; "pygidium" ca. 4 mm long, 1.5 mm wide; "prosoma" ca. 6 mm long and 4.5 mm wide, crossed by two algal strains resembling legs; two "pedipalps" (ca. 5 mm long) present in front of "prosoma."

Remarks.—LACMIP 2504 appears to represent nothing more than a fortuitously shaped stain on the rock, formed around fossils of filamentous algae. Towards the "anterior" end there are diverging structures, which one could interpret as pedipalps while "posteriorly" it vaguely resembles the abdomen of a whip scorpion with a "pygidium" turned almost at right angles, but no telson (Fig. 1). A dark area adjacent to the "carapace" is demonstrably a mass of filamentous algae. Two of the algal strains from this area cross the "carapace" and vaguely resemble two legs on the right side. The two "pedipalps" in front of the "carapace" are a different type of filamentous algal remain. This is also the case for the "carapace," "abdomen," and a roughly triangular unidentified fossil adjacent to the "carapace." These parts of the specimen have a darker color, and frequently express white mineralizations (Fig. 1). They were evidently more robust, organic remains than the filamentous algae. However, there are other similar fossil fragments with these white mineralizations on the rest of the surface of the same bedding plane. One of these in particular is highly likely to be algal or microbial in origin.

Overall, this specimen is organic in nature, but there is nothing to indicate an arachnid. No convincing details of, say, segmentation or the characteristic first leg and pedipalp morphology in a whipscorpion are preserved. Indeed, the Monterey Formation from which the fossil originates is a marine sequence (e.g., Buckeridge & Finger 2001; Saul & Stadum 2005). The flora and fauna of this shale is dominated by the microfossil groups foraminifera, radiolaria, diatoms, and macrofossil groups like filamentous algae, cetaceans, sirenians, pinnipeds, fish, birds, ostracod crustaceans, bivalves, gastropods, bryozoans, polychaetes, leaves, and woody plant debris (Buckeridge & Finger 2001). Limited bioturbation and a predominance of pelagic nekton over benthic organisms suggest a low-oxygen

environment prevailed during much of the middle Miocene. Although the presence of terrestrial flora suggests a whip scorpion could potentially be fossilized in the Monterey shale, this locality has not yielded, for example, a rich insect fauna which would normally be much more common than arachnids. We suggest that *T. hadleyi* is an *incertae sedis* fossil that cannot be assigned to any particular group. It should be excluded from the arachnid fossil record. Thus the only genuine fossil whipscorpions are those from the Pennsylvanian and Cretaceous mentioned above.

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SHORT COMMUNICATION

FIRST RECORD OF *ZIMIRIS DORIAI* (ARANEAE, PRODIDOMIDAE) IN BRAZIL

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ABSTRACT. Spiders of the family Prodidomidae are widely distributed and at least three synanthropic species have been reported. In this work we present the first record of *Zimiris doriai* Simon 1882 from Brazil, appartently introduced accidentally, with specimens recorded in urban areas in the states of Amazonas, Bahia, and Sergipe.

RESUMO. As aranhas da família Prodidomidae apresentam ampla distribuição geográfica e possuem pelo menos três espécies sinantrópicas. Neste trabalho, apresentamos o primeiro registro de *Zimiris doriai* Simon 1882 para o Brasil, como um caso de introdução acidental, a partir de espécimes encontrados em áreas urbanas dos estados do Amazonas, Bahia, e Sergipe.

Keywords: Distribution, Neotropical, introduced species, spider

The spider family Prodidomidae is widespread, occurring on all continents except Antarctica but is more diverse in the southern hemisphere (Platnick et al. 2005; Platnick & Baehr 2006). Prodidomids resemble members of the Lamponidae and Gnaphosidae in having the anterior lateral spinnerets composed of a single article. They differ from lamponids in having enlarged piriform gland spigots, much larger than the major ampullate gland spigots, and from gnaphosids in having the piriform gland spigots greatly elongated (with elongated bases bearing short shafts) rather than widened (Platnick et al. 2005).

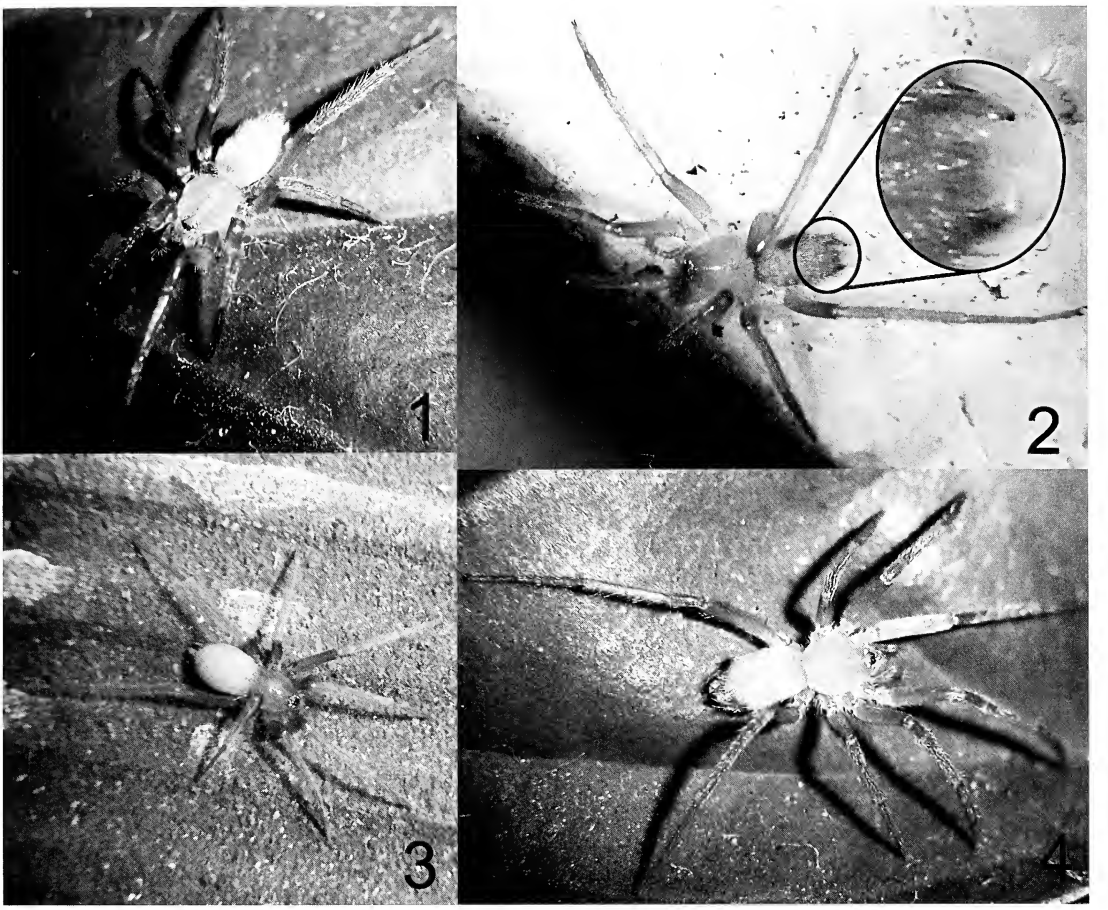
To date, the family Prodidomidae includes 30 genera, of which twelve are known to occur in Central and South America. Only *Lygromma* Simon 1893, *Tricongius* Simon 1893 and *Oltacloea* Mello-Leitão 1940 have been reported from Brazil (Platnick 2007).

Recently, prodidomids identified as *Zimiris doriai* Simon 1882 were collected in Brazil. This species is a fast moving spider, synanthropic and active only at night (Platnick & Penney 2004), which explains its rarity in scientific collections despite its widespread distribution. According to this information and based on its occurrence in synanthropic environments, the first record of *Z. doriai* in Brazil is clearly a case of accidental introduction.

The genus *Zimiris* belongs to the subfamily Prodidominae and its main morphological features are the elongated and widely separated anterior lateral spinnerets (Fig. 2) and also the posterior eyes arranged in a strongly procurved line (Platnick & Penney 2004; Jäger 2005). The genus was recently revised by Platnick & Penney (2004) and currently includes only two species *Z. doriai* and *Z. diffusa* Platnick & Penney 2004, both considered widespread. *Zimiris doriai* (Figs. 1–4) is easily distinguished from *Z. diffusa* by the presence of a bent, sinuous retrolateral tibial apophysis (Fig. 6) and the relatively narrow, retrolaterally excavated conductor (Fig. 5) in the male palp; an omega-shaped rather than triangular epigynal midpiece and longer, narrower paramedian epigynal ducts (Figs. 7, 8) in the female epigynum.

Four specimens of *Z. doriai* were collected in the city of Salvador, Bahia, Brazil and were deposited in the arachnological collections of the Museu de Zoologia da Universidade Federal da Bahia (MZUFBA2066; 32) and Instituto Butantan, São Paulo (IBSP70242; 70243).

The first specimen, a female (Figs. 1, 2), was collected on 11 May 2004, during the day inside a house in the district of Garcia (12°59′29.92″S, 38°30′12.91″W). The second specimen, a male (Fig. 3), was caught on 17 November 2005 during the day inside a house, in the district of Federação (12°59′42.91″S, 38°30′12.91″W). Another male and an immature specimen (Fig. 4) were captured in September 2006 at night inside a house in the district of



Figures 1–4.—*Zimiris doriai*: 1. Female; 2. Details of spinnerets; 3. Male; 4. Immature. Photographs 1, 2, and 4 by Agustín Camacho.

Cabula (12°56′10.45″S, 38°27′54.98″W). Comparing these specimens with other prodidomids of the arachnological collection of IBSP, we detected another three females that were collected in urban environments. Two females were collected in Manaus (2°54′S, 59°58′W), Amazonas (IBSP13883; 23705) inside the lodgings of the Reserva Florestal Adolpho Ducke and the third was found in the city of Aracajú (1°27′21″S, 48°30′14″W), state of Sergipe (IBSP7516).

Zimiris doriai seems to be more widespread than *Z. diffusa,* which is restricted to the Old World. The latter must have been accidentally introduced in many countries of that region. *Zimiris doriai* has been previously reported from India, Cuba, Mexico, Yemen, Eritreia, Sudan, Dominican Republic, Ivory Coast, French Guiana, Malaysia, Java, Massawa (Platnick & Penny 2004), Germany (Jäger 2005), and now in Brazil.

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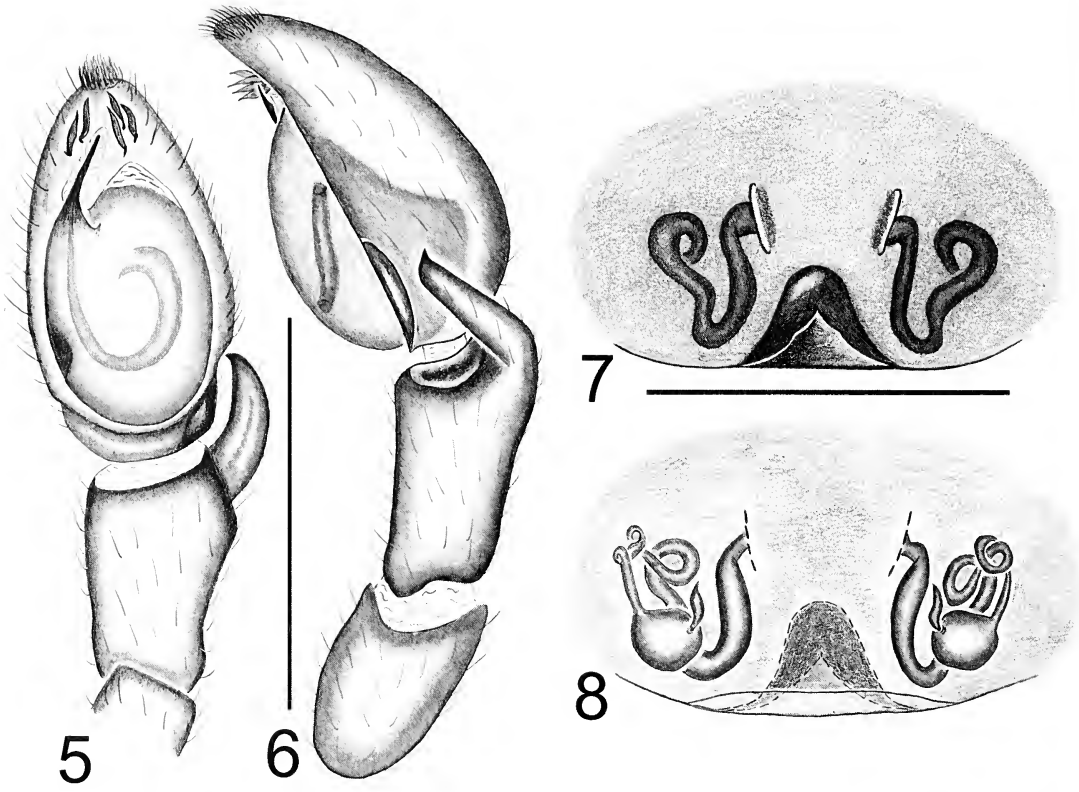

Figures 5–8.—*Zimiris doriai*: 5. Left male palpus, ventral view; 6. Left male palpus, retrolateral view; 7. Epigynum, ventral view; 8. Epigynum dorsal view. Scale: 0.5 mm.

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SHORT COMMUNICATION

CARRION FEEDING BY SPIDERLINGS OF THE COB-WEB SPIDER *THERIDION EVEXUM* (ARANEAE, THERIDIIDAE)

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ABSTRACT. The use of carrion to feed spiderlings has never previously been observed in spiders. Here we show that the theridiid *Theridion evexum* Keyserling 1884 stored dead insectan prey for up to one week prior to the emergence of spiderlings from the egg sac, and continued to feed spiderlings dead prey for six weeks until spiderlings molted to the fourth instar. Spiderlings survived and molted on an experimental diet of exclusively rotten insects.

Keywords: Diet, rotten insects, spiderlings survivorship, prey choice

Generally, spiders are thought to be obligate predators that feed on a wide variety of prey (Bristowe 1958; Foelix 1996). Spiderlings also are predators once they begin to feed (Foelix 1996; GB unpublished data), although the young of some cob-web spiders (Theridiidae) are fed by their mother with freshly caught prey or by regurgitation (Gertsch 1949; Viera et al. 2005). However, numerous examples show that, at least occasionally, spiders in different families feed on carrion (Bristowe 1958; Knost & Rovner 1975; Ross 1981; Pekár 2004), and for some spiders carrion seems to be a primary item in their diet (Sandidge 2003). The use of carrion to feed spiderlings has never previously been observed in spiders, however. Here, we show that mature females of the theridiid *Theridion evexum* Keyserling 1884 begin to store dead prey several days before spiderlings emerge and that spiderlings can survive and grow on a diet of exclusively rotten prey.

Theridion evexum folds a leaf to form a conical retreat, and makes a small tangle just in front the retreat opening (Barrantes & Weng 2007). Several long threads studded with viscid droplets run from this tangle to other leaves. Prey trapped on these long threads are wrapped and carried into the retreat where the spider feeds. The egg sac is housed within the retreat. After emerging from the egg sac, spiderlings remain in the retreat with their mother until they have gone through three or four molts, at which time they disperse. Large young spiders (5^{th} stage to pre-adult), females without spiderlings, and females with new egg sacs will all discard prey carcasses within a few hours. However, frequently females with spiderlings will accumulate several prey items in their retreats (pers. obs.). Observations on feeding behavior and experiments on prey acceptance of *T. evexum* were made in captivity and in the field, from September 2004 to October 2005, in a 2-ha biological reserve on the campus of the Universidad de Costa Rica, San Pedro, San José Province, Costa Rica (9°54′N, 84°03′W; elev. 1200 m).

To determine whether spiders feed on carrion, we fed them flies in the families Muscidae, Calliphoridae, and Sarcophagidae. Flies were killed by placing them in a freezer for 20 to 30 min (−12° C) and were then immediately placed in a chamber saturated with water vapor at room temperature (20–22° C) for 40–54 h for field experiments, or 24–63 h for laboratory experiments. After 24 h the muscles of thorax and legs of the decomposing flies had changed from a nearly white tissue to a juicy, red-brownish mass that emanated a pungent "rotten meat" odor. The dead insects were stuck to the vertical viscid threads of the web, which were then vibrated using a tuning fork or forceps. These movements induced the spiders to descend and attack the dead insect.

Mature female spiders in captivity were each placed on a hexagonal truncated-pyramidal wire frame (20 cm high), with a hexagonal cardboard base (7 cm side) to which the spiders anchored their viscid threads (Barrantes & Weng 2007). A paper cone at the apex of the structure served as the spider retreat. The frame hung 2 m above the floor from a thin nylon fishing line.

To test survival and growth on a diet of rotten insects, we formed nine treatment groups by dividing one clutch of each of three females into three groups of spiderlings that were nearly emerged from the egg

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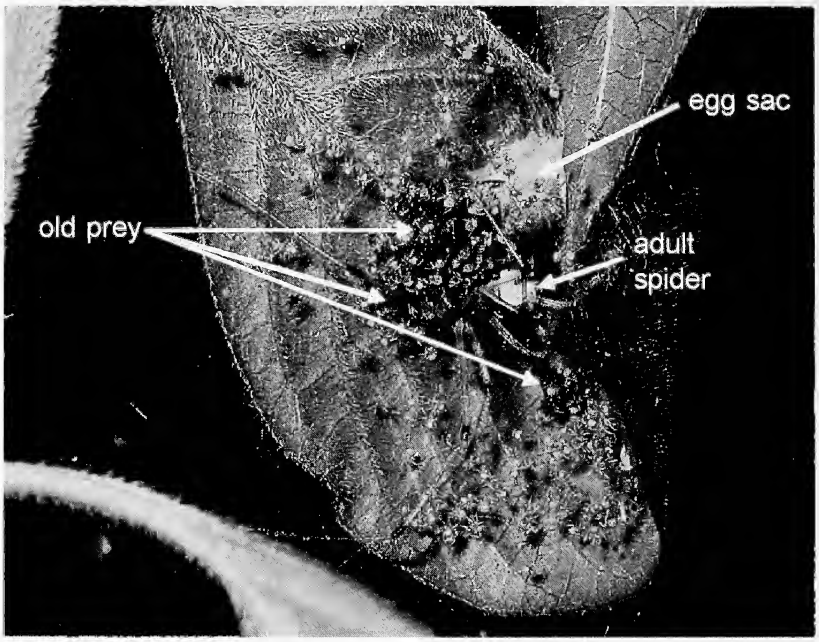
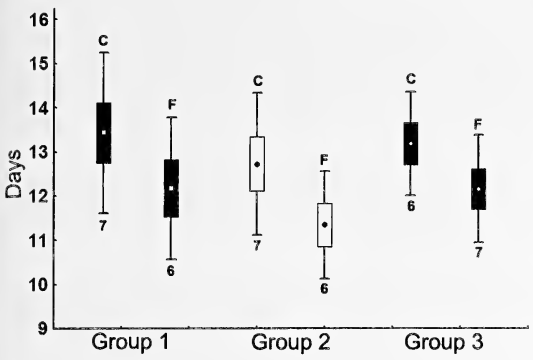


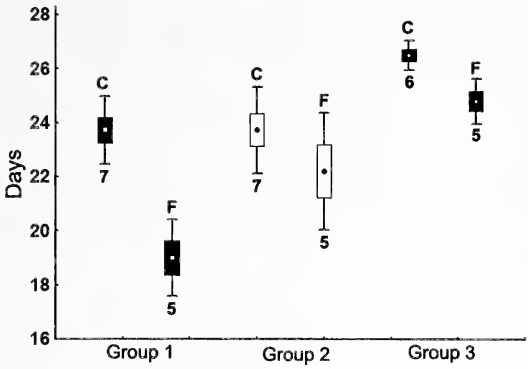
Figure 1.—Mature female of *Theridion evexum* in a retreat that has been opened to reveal the egg sac and the second-instar spiderlings feeding on three dead insects captured two, four, and six days previously.

sac, before they could feed the first time, and placed each group in a separate petri dish (eight groups had seven spiderlings, the other group had six). Spiderlings did not emerge at the same time from the three egg sacs so experiments were not run at the same time for the nine groups. The three treatments were randomly assigned to the groups; thus one group from each clutch was fed rotten insects, the second group, freshly killed insects, and the third group was starved as a control. All insects in this experiment were blow flies (Calliphoridae). Moisture in all petri dishes was provided by a piece of water-soaked cotton. In the rotten-fly treatment, the dead flies rotted at room temperature for 24 h as described previously. Both fresh and rotten flies were pierced four times in the thorax, with an entomological pin, before giving them to the spiderlings. The holes were to facilitate spiderling feeding. Mature females with spiderlings pierced their prey several times, including dead insects, before leaving them for spiderlings to feed upon. We replaced the food for the spiderlings every 24 h and checked for feeding spiderlings three times a day. Instars were counted beginning with emergence from the egg sac (these spiderlings undergo one post-emergent molt inside the egg sac). The intermolt period of the spiderlings to the first and second molts was analyzed using a Randomized Complete Block Design. This analysis of variance allows testing differences among treatments (rotten vs. freshly killed insects) while subtracting the effect of the block (group). Voucher specimens of the spiders were deposited in the Museo de Zoología, Universidad de Costa Rica.

We additionally fed 23 mature female spiders with decomposing insects in the field. Sixteen of these spiders had spiderlings, and both the adult and the spiderlings fed on rotten insects (Fig. 1). Two spiders with egg sacs wrapped the rotten prey and carried them to the retreat where they hung until spiderlings emerged about four days later. The last five females without egg sacs or spiderlings rejected the rotten insects. In captivity we fed three mature females that had egg sacs, from which spiderlings emerged within 10 days, exclusively with rotten prey. When these spiderlings emerged from the egg sac, they and their mothers were fed exclusively with additional rotten insects until some of the spiderlings reached the third instar. These females accumulated carrion for practically six weeks and spiderlings fed on both very old and newly acquired rotten insects (Fig. 1).

Recently emerged spiderlings fed rotten insects (dead for 24 h) and those fed freshly killed flies molted twice (experiment ended when all spiderlings either molted twice or died). However, the intermolt period to the first molt and to the second molt were shorter for spiderlings fed freshly killed insects (first molt, Fig. 2: $F = 7.12$, $P = 0.01$, $df = 1, 35$; second molt: $F = 25.24$, $P < 0.001$, $df = 1, 31$). Surprisingly, all spiderlings ($n = 20$) feeding upon carrion survived, but 28% of the spiderlings feeding on freshly dead prey ($n = 21$) died (*Fisher test* $P = 0.03$). Mortality occurred in all three groups of spiderlings





Figures 2–3.—Intermolt days to the first (Fig. 2) and second (Fig. 3) molt (mean, standard error and standard deviation) of spiderlings fed carrion (C) and fresh prey (F), from clutches of three different females. Sample size is indicated below each subgroup.

fed with fresh-killed flies. All starved spiderlings (n = 21) died before molting a single time.

The results on growth and mortality of spiderlings indicate that bacteria (or other decomposers) possibly reduced nutrient quality and/or content of prey, as the intermolt period to the first and second molt were longer for spiderlings fed rotten insects. However, it is unclear why fresh-killed prey increased mortality of spiderlings. A possible explanation is that bacteria somehow breaks down some proteins (or other components) that could be indigestible, at least for some spiderlings, thus reducing their mortality. Yet, further investigation is needed to understand how the changes produced by bacteria in the prey reduce spiderlings' mortality.

Spiderlings of other theridiid spiders [e.g. *Chrysso cambridgei* (Petrunkevitch 1911), *Achaearanea tesselata* (Keyserling 1884) and *Anelosimus studiosus* (Hentz 1850)] fed occasionally on dead prey accumulated in their webs for up to one week (pers. obs.). However, *T. evexum* is the first spider in which carrion feeding plays a central role in rearing offspring since adult females actively save dead prey for their offspring to feed on. At least in *T. evexum*, *C. cambridgei*, *A.tesselata* and *A. studiosus* the provision of carrion to spiderlings is likely related to the cohabitation of the young spiders with their mother for some time. In these cobweb spiders, spiderlings cohabit with their mother in the same web, at least to the third molt outside of the egg sac (pers. obs.). Saving old dead prey may assure food provision for spiderlings and may be advantageous for maternal spiders as prey is usually unpredictable in time (Wise 1982). It is possible that the use of carrion for adult spiders and as provision for spiderlings may be more frequent when live prey are scarce, as suggested by Knost & Rovner (1975) for wolf spiders.

Spiders of different families have occasionally been observed feeding on dead insects. For instance, Bristowe (1958) reported *Schotophaeus blackwalli* (Thorell 1871) (Gnaphosidae) feeding on dead lepidopterans pinned on setting boards. The ant-eating specialist spider, *Zodarion germanicum* (C.L. Koch 1837) (Zodariidae), apparently occasionally scavenges on dead ants discarded in the cemetery of ant nests (Pekár 2004). *Pholcus phalangiodes* (Fuesslin 1775) (Pholcidae), *Nephila clavipes* (Linnaeus 1767) (Nephilidae) (G. Uhl and W.G. Eberhard pers. comm., respectively) were observed feeding on dead insects hanging for a few days in their webs. Within Theridiidae, three *Latrodectus hesperus* Chamberlin & Ivie 1935, fed on old dead insects (Ross 1981), and four individuals of *Faiditus* sp., a kleptoparasite in webs of other spiders (Agnarsson 2003), were observed feeding on their dead spider host (*N. clavipes*) for more than 16 days (W.G. Eberhard, pers. com.). Knost & Rovner (1975) experimentally demonstrated that wolf spiders (Lycosidae) *Schizocosa ocreata* (Hentz 1844) as well as *Rabidosa rabida* (Walckenaer 1837) and *Rabidosa punctulata* (Hentz 1844) scavenged on old-dead insect parts when freshly killed insects were not available, and Sandidge (2003) described the preference of *Loxosceles reclusa* Gertsch & Mulaik 1940 (Sicariidae) for dead over live prey. It is also known that matriphagy, where spiderlings sometimes feed for several days on their dead mother, is common in several spiders: *Amaurobius* sp. (Bristowe 1958) and *A. ferox* (Walckenaer 1830) (Amaurobiidae) (Kim et al. 2000), *Stegodyphus lineatus* (Latreille 1817) (Eresidae), and occasionally in *A. tesselata* (Theridiidae) (pers. obs.). This fragmentary information on scavenging and matriphagy on a wide, phylogeneticaly unrelated range of spiders (Coddington 2005) indicate that, at least occasionally, carrion feeding is widespread among spiders.

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and G. Uhl for sharing information on spiders' carrion feeding. I. Agnarsson kindly identified the spider.

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REPLACEMENT NAMES FOR TWO ORB-WEAVING SPIDERS (ARANEAE, ARANEIDAE, *ARANEUS*)

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ABSTRACT. The name *Araneus beebei* Levi 1941 is replaced by *Araneus aragua*. *Araneus raui* Levi 1973 is replaced by *Araneus missouri*. The species *Araneus phrygiatus* (Walckenaer 1842) is not recognizable based on the original description and considered a nomen dubium.

Keywords: Nearctic, Neotropical, *beebei*, *aragua*, *raui*, *missouri*

Recent catalogs of spider species names (e.g., Platnick 2007) have made me aware of errors in my naming of two species. *Araneus raui* Levi 1973 is preoccupied by *A. raui* (Strand 1907) for a species from Cameroon and *Araneus beebei* Levi 1991 was previously used by Petrunkevitch 1914 for a species from Borneo. Replacement names are needed:

Araneus raui Levi 1973 [junior secondary homonym of *A. raui* (Strand 1907)], from Missouri, USA = *Araneus missouri* NEW NAME

Araneus beebei Levi 1991 (junior primary homonym of *Araneus beebei* Petrunkevitch 1914), from Aragua State, Venezuela = *Araneus aragua* NEW NAME

Both new names are nouns in apposition after localities.

Platnick (2007) also made me aware of the omission of *Araneus phrygiatus* (Walckenaer 1842) from my revisions of American araneid spiders. The species was cited by Chamberlin & Ivie (1944), with an illustration from a manuscript by Abbot (1792) to which Walckenaer (1842) gave names. Unfortunately I found *A. phrygiatus* to be unrecognizable based on the original description. It was described from Georgia, United States, and is 5 lines (ca. 12 mm) long. The illustration shows an anterior median longitudinal black mark on the abdomen and a broken median longitudinal black line, marks not common in araneids and especially not in species of this size.

Epeira phrygiata Walckenaer 1842, is therefore considered a nomen dubium.

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The late P. Brignoli and N. Platnick's excellent World Spider Catalog made me aware of errors. Allen Brady photographed the plates of the Abbot manuscript in 1963. Also I am obliged to Laura Leibensperger who corrected my writing.

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Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Canadian Journal of Zoology 74:905–918.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66. *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Platnick, N.I. 2008. The World Spider Catalog, Version 8.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/

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Figures 1–4. *A-us x-us*, male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen. Scale = 1.0 mm.

The following alternate Figure numbering is now acceptable:

Figures 1a–e. *A-us x-us*, male from Timbuktu. a. Left leg; b. Right chelicerae; c. Dorsal aspect of genitalia; d. Ventral aspect of abdomen. Scale = 1.0 mm.

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